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NUMBERS 231–264

1965–1967

CAMBRIDGE, MASS., U.S.A.

1967

Edited

By

NELDA E. WRIGHT

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BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. OCTOBER 29, 1965 NUMBER 231

A NEW ANOLE (SAURIA, IGUANIDAE) FROM PUERTO RICO

BY ERNEST E. WILLIAMS,
JUAN A. RIVERO and RICHARD THOMAS

PART I. DESCRIPTION

BY ERNEST E. WILLIAMS
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and JUAN A. RIVERO
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On June 16, 1963, Juan Rivero was collecting at Cerro La Punta at an approximate elevation of 1200 meters when his wife and son, who had separated from the rest of the party, shouted that they had what appeared to be a new species of lizard. The animal was first seen in the axilla of one of the outer leaves of the bromeliad *Vriesia* (*Thecodactyllum*) *sintenisii*, which although usually epiphytic, was growing abundantly, together with *Guzmania berteroniana*, on the forest floor alongside the road. Although the cloud forest is fairly heavy in this area, trees and tree ferns had been cut for about 10 or 15 meters along the margin of the road, leaving an open although somewhat shaded strip on each side. It was in the marginal area between the forest and the cleared area that the new anole was collected.

When capture of the specimen was attempted, it jumped out of the bromeliad and climbed a small bush nearby. The movement was described as slow, but the observers are not certain if it walked, jumped or crawled. Search for other specimens in and out of bromeliads was fruitless.

On July 9, Mr. Francis Rolle collected a second specimen at the Maricao Reserve Forest. The animal was at the entrance of a hole on a partially rotten buttress of a tree at about 1.8 meters from the ground, and 600 to 750 mm from a bromeliad. Mr. Rolle used a fly swatter to stun the animal (which later died enroute) and its behavior could not be observed. Except for its lighter color, this specimen does not differ materially from the type.

The first specimen was kept in the laboratory for several days, but although it was eating well (*Drosophila*) and appeared to be in good condition it was eventually preserved in view of the danger that it might die and decay over a week end when it was not under observation. The animal expanded the dewlap on one occasion, and when given the opportunity to move on the floor, it always did so by jumping, or, if forced to move about until tired, by moving the hind limbs simultaneously, as if it were swimming. A 16 mm black and white film forms part of the type material filed at Museum of Comparative Zoology.

During its first few days in captivity, the new anole slept by lying flat on one of the side panels of the aquarium which served to hold it. All four legs were on the glass, but the tail, on the floor of the aquarium, apparently served to prop the animal upwards. Later, it slept on a twig, in typical *Anolis* fashion. It was never seen to enter a small bromeliad that was provided inside the small tank, but its tail sometimes encircled twigs or small branches with its tip, although the animal was never seen to hang from its tail.

No further specimens were obtained until early 1965 when Richard Thomas and later he and Albert Schwartz collected the new species in numbers at four localities in the mountains of southern Puerto Rico. Thanks to this material more is known both of the habitat and distribution of the new species.

The material of the new species has been divided among a number of institutions: the Museum of Comparative Zoology (MCZ), the American Museum of Natural History (AMNH), the Carnegie Museum (CM), the Museum of Zoology University of Michigan (UMMZ), and the United States National Museum (USNM). A number of the Thomas specimens have been retained in the Albert Schwartz collection (ASFS) or the Richard Thomas collection (RT).

In allusion to its long concealment from scientific record we call the new species by the Latin adjective which means "hidden":

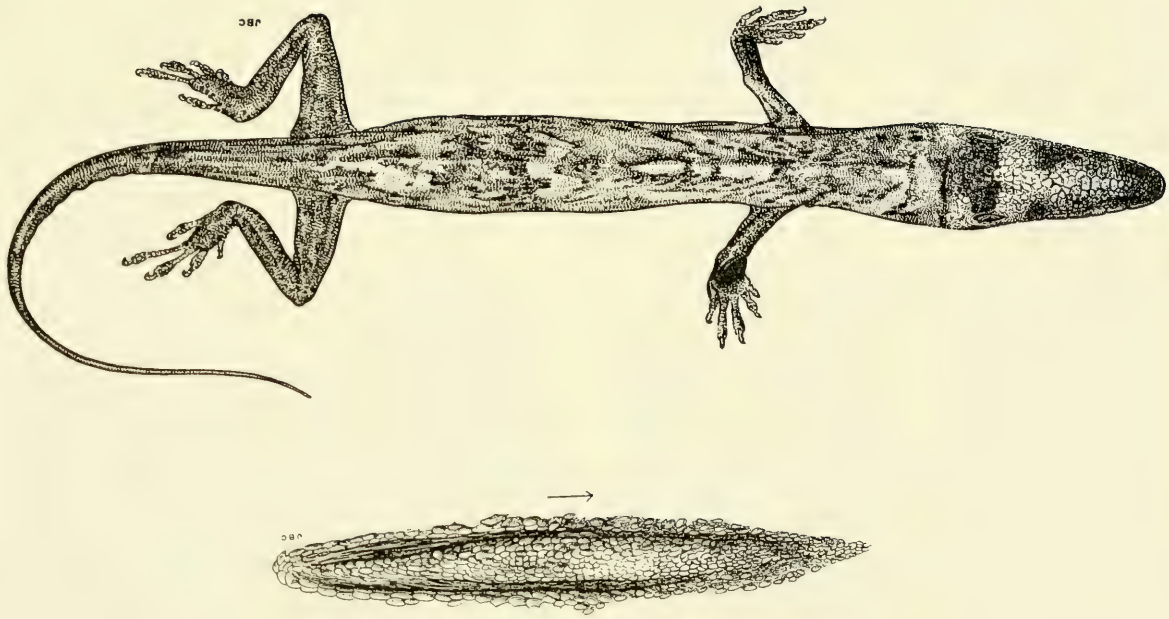

FIG. 1. *Anolis occultus* new species. *Top:* Dorsal view of type, MCZ 80303. *Bottom:* Dewlap of MCZ 83666 (♀) showing inset ("slotted") margin.

ANOLIS OCCULTUS new species

Holotype. MCZ 80303, adult female, on Rd. 143, midway between Cerro La Punta (1338 m) and Cerro Maravilla (1183 m), Puerto Rico, J. Rivero coll., 16 June, 1963.

Paratypes. MCZ 83735, male, *Maricao Reserve Forest,* Francis Rolle coll., 9 July, 1963; ASFS-V5489-91, V5494, AMNH 94560-61, *13.7 km N Sabana Grande,* 2800 feet (850 meters), A. Schwartz, Richard Thomas coll., 25 February, 1965; MCZ 83661-63, same locality, Richard Thomas coll., 28 February, 1965; ASFS-V6196-97, *10.6 km SSE Villa Pérez,* 3400 feet (1040 meters), Richard Thomas coll., 27 March, 1965; MCZ 83664-67, same locality, Richard Thomas coll., 28 March 1965; MCZ 83656, *18.6 km NE Guayama,* 2000 feet (610 meters), Richard Thomas coll., 31 January, 1965; MCZ 83657-59, ASFS-V4891-92, V4901, CM 40691-92, UMMZ 126021-22, USNM 157107-08, *20.9 km NNE Guayama,* 2300 feet (700 meters), Richard Thomas coll., 2 February 1965; MCZ 83660, same locality, Richard Thomas coll., 5 February, 1965; ASFS-V5017-19, same locality, Richard Thomas coll., 3 February, 1965. ASFS-V6662-65, RT 1332, *13.7 km S Palmer,* Richard Thomas coll. 29 July 1965; ASFS-V6670-71, same locality, Richard Thomas coll. 30 July 1965.

Diagnosis. An *Anolis* distinguished from all others by the *wholly granular supraciliary margin,* with no enlarged or elongate scales, and by the extreme reduction of the canthus, of which only the two posterior scales can be said to be differentiated from surrounding scales, as well as by the dorsal scales of the tail which are very small and *smooth.*

Description (paratype variation in parentheses). Head: Narrow, elongate. Head scales small, smooth, *ca.* 13 (9-13) scales across snout between the hardly developed second canthals. A very shallow frontal depression. Nostril oval, nasal scale separated from rostral by one small round scale.

Supraorbital semicircles weakly developed, separated by 2 (2-4) scales, supraocular area with enlarged scales medially, grading into granules laterally. *Entire supraciliary margin granular:* neither any elongate supraciliaries nor any series of enlarged squarish supraciliary scales. *Canthal ridge barely apparent,* its posterior inception indicated by two slightly enlarged squarish scales, hardly larger than the adjacent dorsal snout scales. First two canthals continued by slightly differentiated rectangular scales to a point below the naris. Loreal rows 4 (2-6,

usually 4), all scales subequal. Supratemporal scales subgranular, flattened, grading upward into irregularly enlarged scales surrounding interparietal. Interparietal round, small, larger or smaller than ear, separated from the supraorbital semicircles by 3 (2-6, usually 4) scales. Ear small, subround, placed far ventrally, directly behind the commissure of the mouth.

Suboculars in contact with supralabials, anteriorly grading into loreals, posteriorly grading into supratemporals. Ten to eleven supralabials to the center of the eye, the posterior supralabials very low and small.

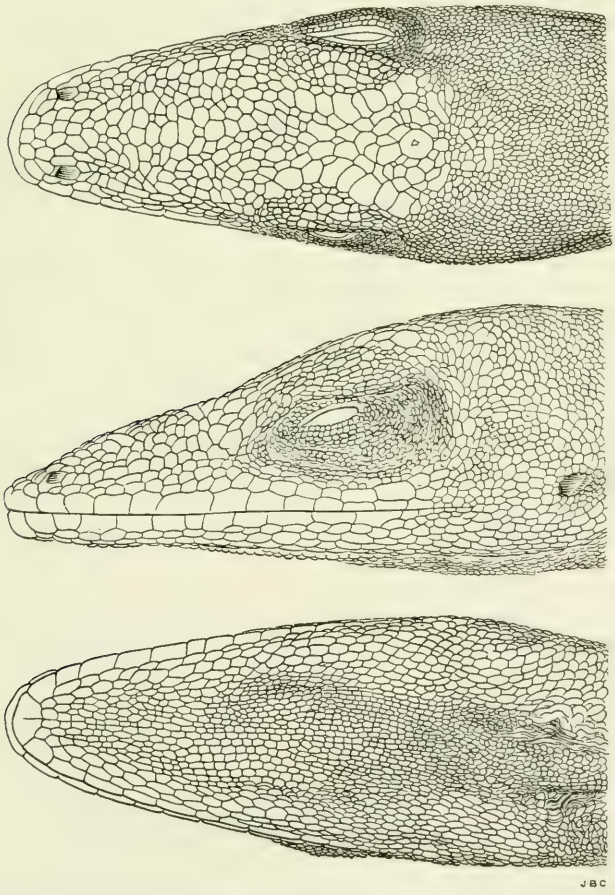

FIG. 2. *Anolis occultus* new species. Dorsal, lateral and ventral views of head of type, MCZ 80303.

Mentals small, about as deep as wide, in contact with 4 (4-6, usually 4) scales between the infralabials. Several rows of throat scales medial to infralabials and posterior to mental somewhat enlarged, grading into granular scales on center of throat; all throat scales smooth.

Trunk: Middorsal scales smooth, flat, not larger than flank scales. Ventrals larger than dorsals, smooth, round, juxtaposed, in transverse rows.

Gular fan: Large, present in both sexes and well developed even in juveniles, lateral margins inset ("slotted") in general skin of neck, all scales granular, smaller than throat scales, much smaller than ventrals, edge scales especially small, lateral scales small but well developed in well separated rows (♀) or these scales weakly developed, or almost absent (♂).

Limbs and digits: Limbs short, flattened dorsoventrally, tibial length not exceeding distance snout-to-middle-of-eye. About 16 (14-20, usually 16) lamellae under phalanges ii and iii of fourth toe. Scales of limbs smooth, much smaller than ventrals, supradigital scales smooth.

Tail: Round, no dorsal crest. No enlarged postanals in males. Scales on dorsal surface very small, smooth, imbricate. Scales behind vent smooth, *ca.* 4-6 ventral rows on distal half of tail, enlarged and keeled. Verticils indistinct, but apparently 11 dorsal granules above, 5 keeled scales below, per verticil.

Color. In the living type the head was gray, with sparse, dark mottles; the eyelids of a lighter, yellowish gray color; general color of dorsum gray, with dark vermiculations and a light bluish cast on the neck region; flanks above the shoulders yellowish green, with black longitudinal spots or vermiculations; rest of flanks yellowish gray turning greenish towards the two extremities; an ochraceous stain on the dorsum, on the midline,

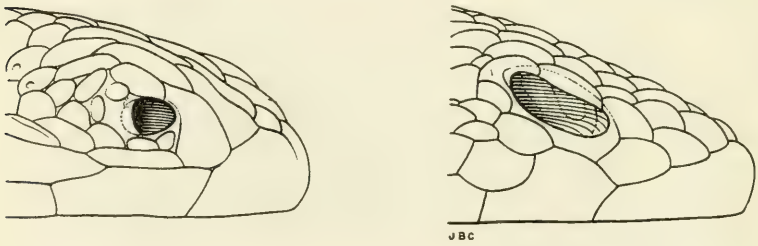

FIG. 3. Scales around nostril compared in *Anolis occultus* (right) MCZ 83661 and *Anolis evermanni* (left) MCZ 61223.

between the anterior limbs; two small, round and well defined yellow spots on each side of the tail base, just below the sacral bones. Below, white, except for some speckling on the throat and tail. The animal could change colors easily, becoming darker or lighter with ease.

The preserved type is of a darker gray color, with lighter reticulation and spotting; there is a light colored frontal band in front of the eyes and a couple of light spots at the base of the tail. Venter and one-third of tail whitish with dark spots and specks, throat with dark areas along the margin of the lip and speckles and spots in the center.

Size (in mm). Holotype: snout-vent, 34; tail 36. Largest specimen: snout-vent, 42.

DISCUSSION

Anolis occultus is far more distinct from other Puerto Rican anoles than a mere tabulation of conventional scale counts and characters (Tables 1 and 2) would indicate. It is a rather

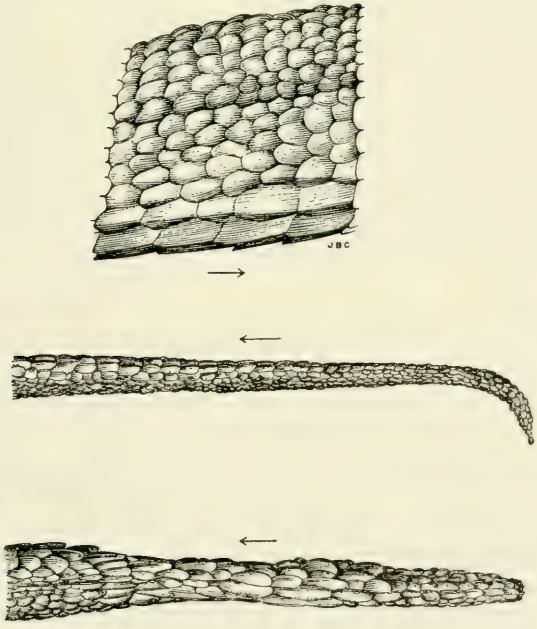

FIG. 4. Tail of *A. occultus*. *Top:* MCZ 83666, a verticil showing typical squamation. *Middle:* ASFS-V 5490, unregenerated tail tip. *Bottom:* ASFS-V 5489, regenerated tail tip.

variable species and therefore approaches or overlaps other species in varying ways (e.g. *gundlachi* in certain characters, *evermanni* in others). It may be helpful to indicate the many ways in which it differs from *all* other Puerto Rican species: It is smaller in maximum size and has a longer head with usually smaller head scales. The nasal scale has not fused with the prenasal scale (Fig. 3). The absence of a differentiated supraocular disk and of elongate supraciliaries and differentiated post-supraciliary rows is very striking (Fig. 2). The mentals are remarkably narrow (as if in *occultus* the apparent first infralabials had segmented off from formerly wider mentals). There are no differentiated sublabials; these are present and large in all other Puerto Rican species. Enlarged postanal scales are absent in males. The tail is weakly if at all compressed and without trace or hint of any dorsal crest (Fig. 4); the dorsal caudal scales are not keeled or enlarged but finely granular and smooth. The dorsal limb scales are granular and smooth, not keeled, and the supradigital scales are also smooth. The fingers, including the distal phalanx, are notably short. The dewlap is sparsely scaled laterally and the lateral skin tucks under the well scaled skin of the throat to give a "slotted" appearance (Fig. 1). (See remarks by Thomas, below.)

It is in fact necessary to go far afield to find species genuinely comparable with *A. occultus*. The suite of living species that requires comparison with *occultus* is the same that required comparison with the recently described *Anolis* in amber — *Anolis electrum* from the Miocene ambers of Chiapas, Mexico (Lazell, 1965) — *A. fuscoauratus, A. chloris, A. maculiventris,* etc.

The Miocene *Anolis*, represented only by its skin, not its skeleton, was remarkable for its small, quite uniform body and limb squamation. In this respect at least — *A. electrum* is unfortunately not complete and many characters are not available — the Miocene anole and *A. occultus* are very similar, and *electrum* might well be, of all known species, the one closest to *occultus*. Of the living species which Lazell compared with *electrum*, the one closest in totality of features to *occultus* is *maculiventris* of the Colombian Choco. As Table 3 shows, in all scale counts there is at least overlap of extremes. Certain differences between *maculiventris* and *occultus* are those associated with the shorter, less tapered head and smaller absolute and relative scale size in *maculiventris*. Thus, in the latter feature, in a larger animal (snout-vent length 42 mm), the body scales are smaller, scales around interparietal smaller, gulars smaller and ventrals much

smaller. Other differences are the presence of a small supraciliary, the wide mental, the unicarinate dorsal limb scales, the multicarinate supradigital scales, the narrower and slenderer digits and the larger caudal scales. The prenasal scale is frequently but not invariably fused with the nasal. The dewlap is not "slotted."

It is not at all probable that *occultus* is close to *maculiventris*, but the necessity of comparison with a mainland species geographically so distant emphasizes the very isolated position of *occultus* in the West Indies. Resemblance to *maculiventris* and to *electrum* may indicate preservation in *occultus* to a greater or lesser degree of a primitive anoline squamation pattern. This, however, is a point which will receive attention in a separate paper in which these and the osteological characters of this strange new Puerto Rican anole will be analyzed at length and their implications assessed.

No detailed discussion of the distribution of *occultus* in Puerto Rico is possible. It has been collected at the two extremes of the Cordillera Central and with all probability will be found wherever the proper habitat exists all along this range. It has been recorded also by very recent collections (July 29-30, 1965) on El Yunque. All present records are above 600 meters.

One comment more must be made. The discovery of so distinct a species in an island thought to be well known herpetologically and in which the anoles have received special attention must give us pause. As will appear from the observations reported below by Thomas, *A. occultus* is a creature of the canopy. We may well be ignorant of many another species of the canopy on the islands and on the mainland.

ACKNOWLEDGMENTS

We are indebted to Mr. Richard Thomas and Dr. Albert Schwartz for the privilege of examining the more than 30 specimens collected by Mr. Thomas, and to Mr. Francis Rolle for the gift of the specimen collected by him. Permission to quote certain numerical data on Puerto Rican *Anolis* from an unpublished thesis has been granted by Dr. A. S. Rand. The illustrations are by Joshua Clark. This study has been supported by National Science Foundation Grant GB-2444.

LITERATURE CITED

Lazell, J. D. Jr.

1965. An *Anolis* (Sauria, Iguanidae) in amber. Jour. Paleont. **39:** 379-382.

PART II. FIELD OBSERVATIONS ON *ANOLIS OCCULTUS* WILLIAMS AND RIVERO

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Having been fortunate enough to collect the first substantial series of the newly described *Anolis occultus*, I take the opportunity to present those observations on habits, habitat and color repertory which were made incidentally to collecting the specimens. I am indebted to Dr. Albert Schwartz, without whose support the collections would not have been made, and Dr. Ernest E. Williams whose advice was to be alert for a strange and new little anole in the forests of Puerto Rico.

All but two specimens of *occultus* collected by me were taken at night while they slept. They invariably slept on dead or leafless vines and twigs. Although the sleeping sites were usually associated with a viny or bushy tangle, frequently individuals slept on single branches which projected beyond the main mass, or on pendant pieces of vine. While sleeping (Fig. 5) the head

Fig. 5. Typical sleeping posture of *Anolis occultus*.

was almost always towards the distal part of a twig or vine (where this could be determined). The forelimbs were flexed and the hindlimbs extended along the sleeping surface only slightly flexed. At times the fifth toe was positioned against the tail on either side, as if to hold it in place (a posture seen in some "grass anoles"). The tail was curled loosely about the vine or twig to a varying extent, sometimes completely encircling it. This characteristic prehensility of the tail enabled specimens of *occultus* to be identified at a glance even at a distance that would

not ordinarily allow positive identification of so small a lizard. No specimens were ever observed sleeping on leafy portions of plants, whether green or dried, despite the abundance of ferns and grasses, and shrubs, at all the localities.

When grasped, these lizards characteristically held tightly to the sleeping surface, and it was frequently simpler to break off the vine or twig on either end of the specimen than to risk injuring it by pulling it off. Typically, they showed great tolerance to shaking and disturbance of their sleeping sites. When dislodged with a stick they might fall a short distance but adroitly catch themselves on the next object in their path, simultaneously assuming the sleeping posture. On two occasions specimens were disturbed sufficiently (by approach of the collector with flashlight, not by being shaken) that they suddenly released their hold and dropped. One was recovered when it was found resting immobile in a tangle of vegetation on the ground.

Williams and Rivero have commented on the slow movement reported by the collectors of the first specimen of this species. It is my observation that movement was "not slow but had a desultory aspect, not a hasty scampering characteristic of so many anoles" (field notes on specimen collected during day). The relatively short limbs of this species probably account for this apparent lack of haste or a leaping mode of progression. I have seen specimens of this lizard confined in a plastic bag make short hopping movements, but in the field evasion took place as a fast walk from stem to stem. When progressing over a uniform surface (along a smooth stick, for instance), an almost salamander-like crawl is employed.

When caught or handled, *A. occultus* may emit a rather persistent squeaking during its struggles to escape. On two occasions captive specimens were observed displaying the dewlap. In the admittedly artificial environment of a plastic bag filled with a coil of dead vines, the specimens displayed from a horizontal position with little flexure of the head and neck.

The dewlap of this species, when retracted, appears to fit into a longitudinal slot in the throat and anterior chest. This is a characteristic of living specimens and is not an artifact of hardening in preservative. This "slot" (which is not evident when the dewlap is extended) is in the form of a distinct invagination of skin on either side of the retracted dewlap; the folds on each side meet posteriorly and the entire structure is

FIG. 6. Diagrammatic cross-section of a situation similar to those encountered at localities 2 and 4. The dotted lines indicate the approximate zones where *occultus* was seen; the vertical line equals an approximate height of six feet.

elongate and U-shaped. The posterior part of the dewlap inserts beneath the "U" portion of the fold. The feature is present in even the smallest specimens.

In life the eyes are chameleon-like: "very protuberant and capable of considerable movement in all directions; some degree of independent movement was evident" (field notes).

Locality 1: 18.6 km NNE Guayama, Puerto Rico, 2000 feet (610 meters), 1 specimen. The first specimen of *Anolis occultus* collected by me was found on a broad-leafed green plant growing in an open, sunny spot along the side of a path through montane rain forest. The specimen was on the upper surface of a leaf and moved to the under surface of an adjacent leaf when approached. Subsequent search at this locality both day and night yielded no other specimens.

Locality 2: 20.9 km NNE Guayama, 2300 feet (700 meters), 16 specimens. At this locality there was a path cut into a forested hillside (Fig. 2). The forest grew close to the sides of the path and in places overhung it. Downhill from the path grew what may be called the forest proper, which in places leveled off after a short drop. Above the path grew a dense second growth of generally smaller trees, ferns and viny tangles. *A. occultus* was found sleeping at night in tangles of dead (or leafless) vines and twigs along both sides of the path, four to ten feet above the ground (i.e. above the path on the uphill side, which includes the height of the cut-bank, or above the slope directly below the specimen on the downhill side).

All but one specimen taken at this locality were collected at night while they slept. Specimens invariably slept on dead or leafless vines and twigs.

An attempt to collect *occultus* in the forest below the path failed. The apparently preferred sleeping places were abundant enough, but all these were well below the canopy of the forest and not exposed by breaks in the forest.

A brief stop was made at this locality during the daytime. One specimen was seen resting on the underside of the tip of a dead fern leaf, where it had possibly retreated at my approach.

Locality 3: 13.7 km N Sabana Grande, 2800 feet (850 meters), 9 specimens. This locality was a region of montane rain forest of the same general composition as the first two localities but with a lower canopy. Specimens of *occultus* were found along paths through the forest but not of the 'cut bank' sort reported for the second locality. Specimens were definitely associated with an opening in the canopy. Where the forest canopy completely closed over the paths, *occultus* was not to be found, despite the apparent abundance of the required viny tangles. The forest in this area was relatively low, so that there was not so large a space between the canopy and the ground. Specimens were found sleeping in similar situations to those of the second locality at heights above the ground of approximately four to ten feet. Three specimens were seen which were not collected due to the height at which they were sleeping (about 15 feet). One of these remained in place until the dead vine on which it rested was broken by being rather violently shaken.

Locality 4: 10.6 km SSE Villa Pérez, 3400 feet (1040 meters), 8 specimens. Here specimens were collected in a situation very similar to the second locality. A path cut into a hillside wound

through about two kilometers of montane forest. Specimens were collected at night as they slept. All were taken in an area where the downhill woods were high enough to partially or, in spots, completely enclose the path. Even under intensive search, specimens were not found in areas where the forest had been cleared below the path or the vegetation was low and sparse, even though the vegetation above the cut bank was of the proper type and density. The lizards slept at heights of about five to twelve feet above the ground.

A visit was made to the Dona Juana Insular Forest, where no specimens of *occultus* were seen. The forest at this locality was very high and the canopy consequently out of easy access or sight. Likewise, the Toro Negro Insular Forest yielded no specimens, no doubt because of the lack of enough accessible situations in which the species is most easily collected.[1]

From the foregoing observations it is seen that *A. occultus* prefers as its sleeping site (and this should be a fairly good indication of its general habitat preference, though slightly more restricted) dead or bare twigs and vines in areas of close forest in the proximity of small breaks in the canopy. Normally, of course, the canopy is not accessible to the collector. It appears to be only in certain situations (breaks in the forest which allow, in effect, a descent of the canopy to a low level) that these lizards are accessible. It seems not improbable that *occultus* is normally a lizard of the canopy, demanding a thicket of bare vines and twigs among the foliage with readily available exposure to the sky. The possibility that it might be simply a clearing-edge anole is not indicated by my collecting experience. Specimens were not found along the edges of forest adjacent to large clearings or wide roads.

At the first locality two other species of anoles were collected, *A. gundlachi* and *A. evermanni*. Both of these lizards are essentially "tree anoles" of forested regions; the former is primarily a species of deep shade, the latter is often found on herbaceous plants such as *Heliconia* and *Musa*, but it is by no means restricted to such situations. At the second locality specimens of

[1] Since this manuscript went to press, another visit was made to Puerto Rico where seven more specimens of *A. occultus* were collected in the El Yunque region. All were taken at night along a path on a forested hillside, a situation very similar to that described for localities 2 and 4. One specimen was found sleeping on the edge of a vertically oriented green leaf.

A. cristatellus and *A. krugi* were collected; *gundlachi* and *evermanni* were also seen there. *A. krugi* is an anole of bushes and grass and is sometimes almost terrestrial in habits. Its sleeping site preferences are less restricted than those of *occultus*. It may sleep on green or dead plants, leaves or stems, and is much less particular about how it positions itself. At locality 3 only *A. gundlachi* was collected in addition to *occultus*. At locality 4, *cristatellus* and *krugi* were taken; *gundlachi* was seen. *Krugi* was very common there and during the day was often seen running through the grass along the more open parts of the path. In addition, a juvenile specimen of an as yet undetermined species of large anole was collected at this locality.

COLOR REPERTORY

Anolis occultus possesses a well developed and complex disruptive pattern which is variously manifested in different color stages. In its complete development, the pattern consists of the following elements: a dark cephalic figure or interocular triangle, which may be solid or hollow; a pattern of dark radiating eye lines; four zones of transverse banding on the body (scapular, dorsal, lumbar, and sacral) which may be manifested as either very hazy, indistinct dark bands or as bands with a sharply defined, sinuous, dark anterior edge and a posteriorly fading zone of dark pigment; a lumbar spot (occasionally paired), which is present in the lumbar band but is frequently evident when the band is not and is perhaps the most constant pattern element; a fine reticulum of dark lines, which frequently appears as faint small ocelli. The venter is light, frequently with some stippling and a distinct but irregular zone of juncture with the dorsal coloration. The transverse body banding continues onto the tail as small dark chevrons.

The colorations displayed by this lizard may be characterized as follows:

Unicolor: Varies from gray through olive-brown, olive, yellow-green to a dirty orange color. Pattern elements are minimal in this range of phases but parts of the major elements may be present; the lumbar spot is usually present. Axillary and inguinal areas may be a dull or bright yellow; a yellow edge to the lumbar spot may be present. This phase is the predominant one seen in specimens in the wild, which are usually green in the daytime and gray or brown at night.

Lichenate: The pattern is boldly developed and black or dark gray; the ground color is off-white or very light gray. This presents a very complex, striking and disruptive pattern; it is perhaps a "fright" pattern as it is often seen in freshly collected or killed specimens.

Intermediate: This category covers a wide range of effects intermediate in various combinations between the other two. The pattern may be well developed and the ground color various shades as seen in the unicolor phase; the pattern may be fragmented, moderately or poorly developed with various shades of ground color, commonly brown, yellow-brown or gray. A frequent variant is almost uniformly reticulate above with especially prominent dark diagonal lines in the neck and scapular region.

Dewlap color: The dewlaps were frequently noted as being pinkish gray. An individual whose dewlap was color-noted (ASFS V4890) with the Maerz and Paul Dictionary of Color (1950) was keyed to Plate 7E7. The posterior edge of the dewlap was rusty. This coloration was typical of the other specimens.

LITERATURE CITED

MAERZ, A. and M. REA PAUL

1950. A dictionary of color. New York, McGraw-Hill Book Co., pp. i-vii, 1-23, 137-208, 56 pls.

(Received 29 June 1965.)

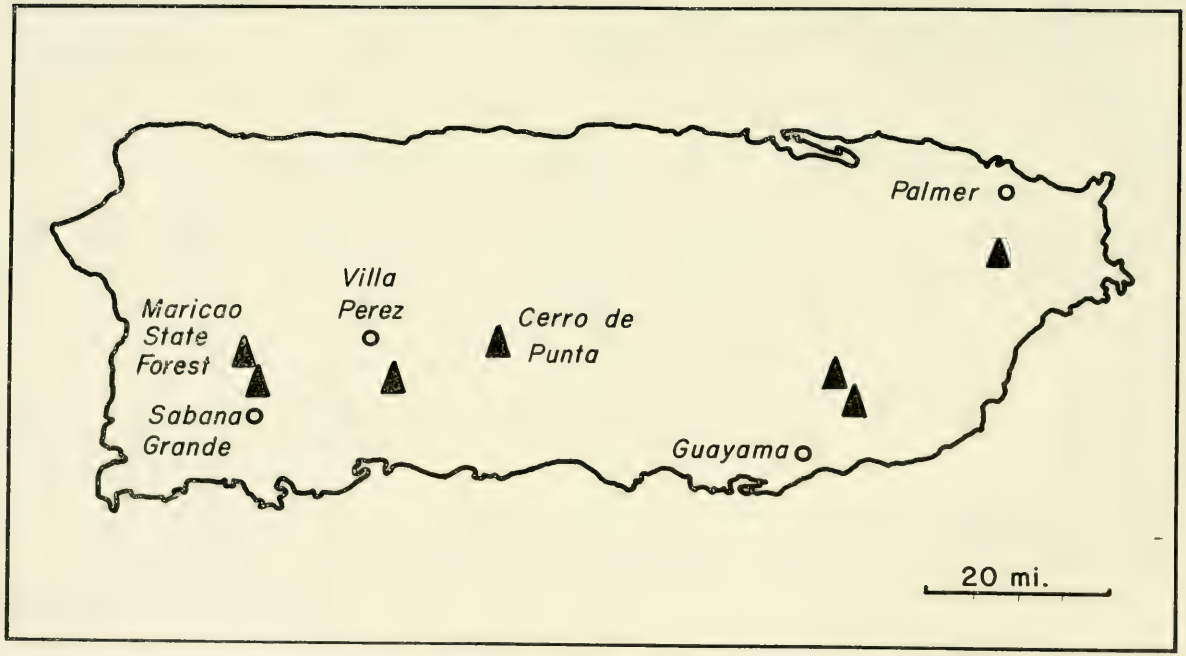

FIG. 7. Distribution of *Anolis occultus* new species in Puerto Rico. Black triangles indicate the known localities. Open circles indicate towns.

Table 1

Scale characters in Puerto Rican *Anolis*

Anolis	S-V length (mm) adult ♂	lamellae 4th toe	scales across snout at second canthal	loreals	labials to center of eye
occultus	34	14-18	9-13	2-6	8-13
cuvieri	126	31-33	8-9	6	7-8
evermanni	60-70	25-30	4-6	4-6	5-7
stratulus	44-48	22-24	4-7	3-6	5-8
cristatellus	65-74	22-25	4-7	5-7	5-7
gundlachi	58-69	18-22	7-10	6-10	5-8
krugi	45-55	21-23	4-7	6-7	6-8
pulchellus	45-50	19-21	4-5	3-5	5-7
poncensis	43-46	18-21	4-6	3-5	5-6

Table 2

Scale characters in Puerto Rican *Anolis*

Anolis	scales between semicircles	interparietal from semicircles	middorsal rows enlarged	ventrals	tail crest
occultus	2-4	2-6	0	sj	—
cuvieri	3	3	1	si	+ !
evermanni	0-1	1-4	0	si	(+)
stratulus	0-1	0-3	0	si	+
cristatellus	0-1	1-4	2	s/k, i	+ !
gundlachi	1-3	3-8	2	ki	+ !
krugi	0-2	1-5	4-6	ki	(+)
pulchellus	0-2	1-5	*ca.* 12-18	ki	(+)
poncensis	0-1	1-2	*ca.* 16-20	ki	(+)

s = smooth ; k = keeled ; i = imbricate ; j = juxtaposed ; ! = strong ; ( ) = weak.

Table 3

Scale character comparison

	maculiventris	*occultus*
scales across snout at second canthal	9-16	9-13
scales bordering rostral posteriorly	6-9	5-9
scales between semicircles	2-4	2-4
loreal rows	6-9	2-6
interparietal from semicircles	5-10	2-6
labials to center of eye	6-9	8-13
scales bordering mental between infralabials	5-8	4-6
fourth toe lamellae	15-18	14-18

BREVIORA

Museum of Comparative Zoology

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HISPANIOLAN GIANT ANOLES (SAURIA, IGUANIDAE): NEW DATA AND A NEW SUBSPECIES

By ERNEST E. WILLIAMS

Recent collections of Hispaniolan giant anoles (*Anolis ricordii*) by Albert Schwartz and his co-workers, and smaller numbers of specimens procured by Luc and George Whiteman for the Museum of Comparative Zoology, fill in many of the gaps in the distributional record (Williams, 1962) and permit formal description of a new race.

This study has been supported by National Science Foundation Grant GB 2444.

The material of the new race has been divided at Dr. Schwartz's direction between the Museum of Comparative Zoology (MCZ), the American Museum of Natural History (AMNH), and his own collection (ASFS). A single specimen from the collection of Donald W. Buden (DWB) has been examined through the courtesy of Dr. Schwartz.

The new material confirms the taxonomic utility of the scale characters previously employed in the analysis of geographic variation (Williams, 1962). However, although Dr. Schwartz has generously made available field notes on colors in life, variation in color and pattern is such, and there is such a repertoire available to any single individual, that the hesitations and cautions expressed in the 1962 paper on this subject seem still very pertinent. The attempt has been made to use color data as fully as possible, but it will be apparent in the following pages that I have succeeded only to a limited degree. While I have described below a new subspecies primarily on color pattern, I do so with the explicit admission that only crass differences in pattern or pattern repertoire seem at all usable.

It is easiest to confront the new data in terms of the major distinguishable populations — i.e. the subspecies. I have therefore begun with the nominate race:

ANOLIS RICORDII RICORDII Duméril and Bibron

New Records: **Haiti.** *Departement de l'Ouest.* Lancerouelle near Mirebalais, MCZ 69404; Mirebalais, MCZ 68479; Saltrou, MCZ 69405.

Dominican Republic. *Monte Cristi Province.* Laguna de Salodillo, 7 km SE Pepillo Salcedo, ASFS V 1470; 1 km W Copey, ASFS V 1269, V 1411–12, V 1470.

The new specimens indicate that this race, in addition to occupying all of Haiti north of the Cul de Sac Plain, extends into the Dominican Republic in the Monte Cristi region. Hence the suggestion (Williams, 1962) that Ti-Guinen just west of Cape Haitien on the north coast of Haiti might be an intergrade area is in error. The *extent* of black on the head, nape, and shoulders of *ricordii ricordii* is apparently individually variable to a greater extent than I then realized and is perhaps less evident in the live animal than in the preserved animals. The presence of intense black patches on the anterior body and head is still a strongly marked characteristic of the males of this subspecies and is strongly correlated with the very low nape and dorsal crest scales, as well as with a high number of scales across the snout at the second canthal.

One character not previously available has been the color of the dewlap. The dewlap in the Monte Cristi specimens is described as ranging through pale peach and brown, pale peach, very pale peach speckled with brown proximally to pale yellowish gray.

Despite the new collections one embarrassment remains. No certain intergrades between the two strikingly different forms *ricordii* and *baleatus* are yet known. In view of the erratic occurrence of these giant anoles and the usual difficulty of collecting a series (see, however, below for Camp Perrin in southwest Haiti), it is not completely surprising that this should still be true. However, the area in which intergrades may occur is being narrowed: on the north coast of the Dominican Republic between Monte Cristi and Santiago and in the center of Hispaniola between Mirebalais (MCZ 68479, 69404) and Santiago. This still leaves a very wide area of ignorance.

A single specimen from Saltrou (MCZ 69405) narrows the geographic gap between *ricordii ricordii* and *r. barahonae;* however, it does nothing to narrow the character gap. This is a male extremely heavily marked with intense black not only on nape and back of head but also on the flanks — more heavily than any other specimen; in squamation also it is quite typical of *ricordii.*

Dr. Schwartz (pers. comm.) reports taking the Monte Cristi series in vines at night in a wooded area about a small cattle pond

between Copey and Pepillo Salcedo — an otherwise arid region. He states that in general *ricordii* can be captured with moderate regularity while sleeping at night in viny tangles, especially where there are dense "mats" or "curtains" of vines under a canopy. This is a usually reliable technique which, however, sometimes fails; there may be areas in which the species just does not occur.

Anolis ricordii baleatus Cope

New records: **Dominican Republic:** *La Vega Province.* 4 km SW El Rio, ASFS X 8558; 0.3 mi (0.5 km) E El Rio, ASFS X 8114; 12.8 km NW Bonao, *ca.* 1200 feet (360 m), ASFS V 4317. *Puerto Plata Province.* 11 km SE Sosua, ASFS V 1717. *Duarte Province.* 5.6 km SW San Francisco de Macoris, DWB 271; *ca.* 4 km NE Ponton (Rio Cuaba), ASFS V 2987. *Samana Province.* 6 km E Sanchez, ASFS V 1904. *Peravia Province.* 1.1 mi (1.8 km) S San Jose de Ocoa, 1400 feet (425 m), ASFS V 723. *El Seibo Province.* 3.5 mi (5.8 km) S Sabana de la Mar, ASFS X 7877; 2.1 mi (3.5 km) N El Valle, ASFS V 7861–62; 3 km N El Valle, ASFS V 3157–58. *La Romana Province.* 0.7 mi (1.2 km) W Higuey, ASFS V 854–55; 1 mi (1.7 km) W Higuey, ASFS V 1038; 2.5 km NW Boca de Yuma, ASFS V 1136; 0.5 mi (0.8 km) NW Boca de Yuma, ASFS V 961–62.

The new specimens of *baleatus* add no critical localities; only the eastern Dominican Republic is represented. No qualification of the characters previously reported for this race is required; the squamation characters show a very limited variability.

Again, the colors of dewlap and chin may be added as new characters. The dewlap is described as "orange" (adult ♂), "dark orange" (adult ♂), "very bright orange" (adult ♂), "dull grayish orange" (adult ♀), "dirty orange" (adult ♀), "orange brown" (adult ♀), "pale grayish orange" (juvenile ♂), "dewlap skin charcoal, scales yellow-green" (juvenile ♀). The chin of the male from southeast of Sosua, Puerto Plata Province, with a bright orange dewlap is described as having the chin bright orange also. Other males from El Seibo Province, La Romana Province, and La Vega Province are described as having the chins some shade or other of green, varying from dark green through mottlings to yellow green. The significance of these differences is at present quite obscure; it would be particularly important to know the individual powers of color change.

Anolis ricordii barahonae Williams

New records: **Dominican Republic.** *Barahona Province.* 8 km SE Las Auyamas, 2600 feet (7880 m), ASFS X 9676. *Pedernales*

Province. 13.1 mi. (21.8 km) SW Enriquillo, ASFS V 4422.

One new specimen from 8 km SE Las Auyamas, Barahona Province, which is quite near Polo, is almost topotypic and adds no new information. As in typical specimens, the dorsum has obscure, irregular, dark blotching. The lower flanks are boldly blotched black on white. Blotching here is usual but is not usually so bold.

A second — ASFS V 4422 — from 13.1 miles (21.8 km) SW of Enriquillo, Pedernales, is typical in squamation but peculiar in having very distinct small *light* spots on the flanks. The color in life of this specimen is given by Schwartz in his field notes as: "Dorsal ground color brown to grayish, with white (faintly bluish) dark-edged ocelli. Venter white with gray mottling and stippling. *Dewlap pale yellow, pink along outer edge.* Head light brown. Soles of hands and feet pale yellow."

It will be recalled that it was a specimen from Enriquillo (AMNH 51241) that caused some hesitation when *barahonae* was first described. In AMNH 51241 the pattern was thought to be obscure banding; the present specimen clearly shows spots tending to be vertically aligned — a condition which is easily transformed into vertical banding. It is possible that the *ricordii* populations in the vicinity of Enriquillo consistently show a distinctive pattern though characteristically *barahonae* in squamation.

Anolis ricordii leberi new subspecies[1]

Holotype: MCZ 80935, adult male from Camp Perrin, Haiti, native-collected for Albert Schwartz, 26 July 1962.

Paratypes: MCZ 80936–42, 83982, AMNH 93713–21, ASFS X 3033–35, 3038–39, 3041–42, same data as type; MCZ 80943–53, AMNH 93722–36, ASFS X 3182, same data as type except collected 28 July 1962.

Diagnosis: A subspecies of *ricordii* resembling *barahonae* in the size of the scales of the snout (4–6 across snout between second canthals) and in the slender, tapering, but small scales of the nuchal crest, but differing from *barahonae* in the higher and larger dorsal crest scales and in the presence in adults of both sexes of a pattern of bold alternating black and light lines on nape and flanks, the black lines more or less broken into and complicated by light cross-banding. (One or two specimens have this pattern very much reduced and juveniles are irregularly spotted, without light or black lines.) Dewlap in life is a rich yellow.

[1]Named for David C. Leber who has prepared accurate and beautiful water color portraits from life of this and many other West Indian anoles.

Fig. 1. *Anolis ricordii leberi*, new subspecies. Black and white from a water color by D. C. Leber.

Comments. Almost all specimens show the broken linear pattern quite clearly; probably all adults would do so in the darker phases of their pattern repertoire.

So large a series from a single locality is quite extraordinary for any of the giant anoles. Albert Schwartz (pers. comm.) confesses that *none* were seen by himself and coworkers during the period in which this splendid sample was collected by local people. A. S. Rand (*in* Williams, 1962) has commented on the shyness and difficulty of catching the single individual of this same species which he saw in 1960. Obviously only the diligence of the local Haitians has permitted this glimpse of the real numbers of these anoles which, as inhabitants of a tree crown habitat, usually elude the general herpetological collector.

From the point of view of the study of the geographic variation to which subspecific names are expected to call attention, a sample from one locality, however large, is not ideal.

The single specimen from outside the Camp Perrin region which is referred to *leberi* — MCZ 38277, collected by P. J. Darlington, Jr., discussed in Williams, 1962 — has not been made a paratype of the new taxon. It is a juvenile which in squamation completely agrees with *leberi*. However, while in its spotted, non-lineate pattern it is roughly like the single topotypic juvenile available (MCZ 83982), the pattern agreement is not striking enough and the preservation (showing an odd purplish tone not seen in any other specimen) is too different for confident assignment of the animal.

The Darlington specimen is from Tardieu in the Massif de la Hotte, not far west of Camp Perrin, but this portion of the southwest peninsula of Haiti is a region of Hispaniola in which sharp character changes occur in other anoles (e.g. *distichus*, *cybotes*) within very short distances. It is a region also which, except for the road connecting Les Cayes and Jeremie on which Camp Perrin lies, is largely herpetologically unknown. It cannot be cavalierly assumed that only one *ricordii* race will be native to this area. Perhaps no surprises await us, but in the West Indies sharp faunal changes are not unusual and casual generalizations are never safely made.

REFERENCE CITED

Williams, E.E.
1962. Notes on Hispaniolan herpetology. 6. The giant anoles. Breviora, Mus. Comp. Zool., No. 155: 1–15.

(Received 29 June 1965)

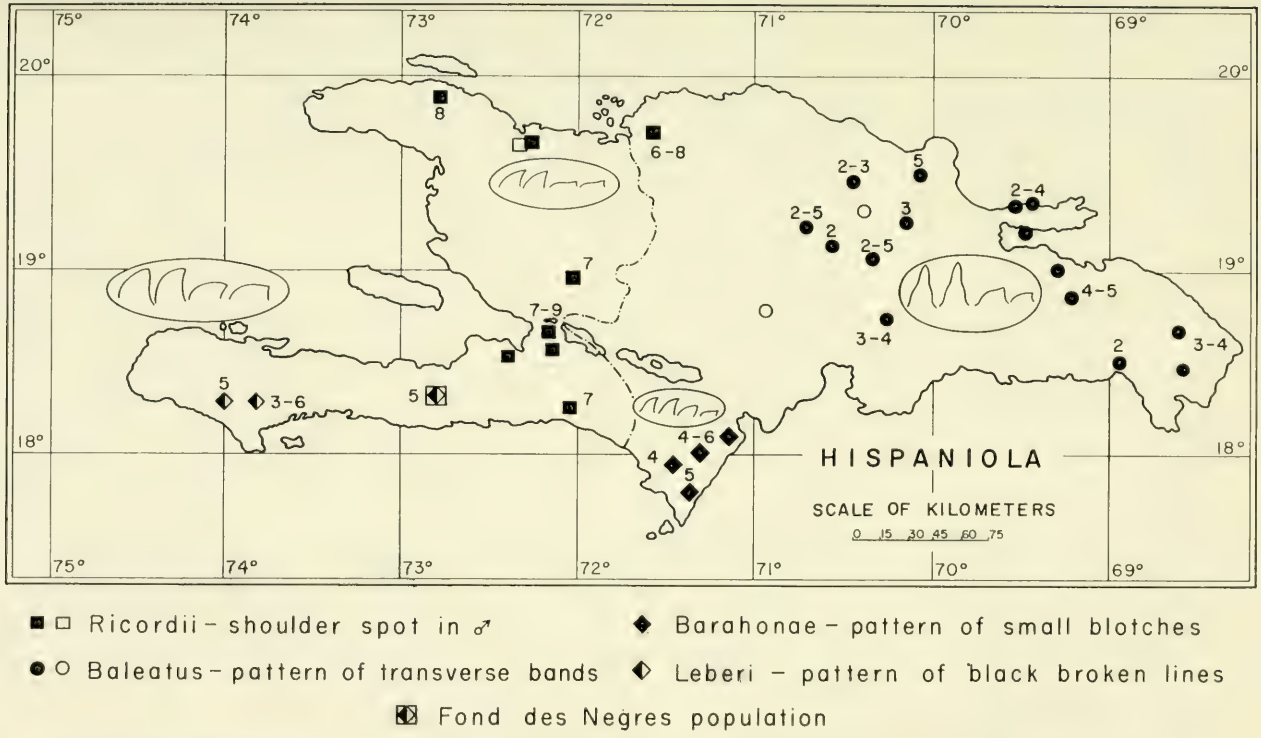

Fig. 2. Revised distribution map of *Anolis ricordii* subspecies. Hollow symbols for *ricordii* and *baleatus* are Mertens' records. In each oval is represented, left to right, the outline of two nuchal scales and two dorsal scales. Numbers are counts of scales across snout in populations indicated by adjacent symbols.

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SOUTH AMERICAN *ANOLIS* (SAURIA, IGUANIDAE): TWO NEW SPECIES OF THE *PUNCTATUS* GROUP

BY ERNEST E. WILLIAMS

Anolis punctatus Daudin is the earliest discovered, most widely distributed, and morphologically the central member, of a group of forest anoles in South America. The males of *punctatus* (and of its race *boulengeri* O'Shaughnessy) have the rostral swollen, projecting strongly beyond the lower lip. This is the first adumbration of a condition which becomes weirdly emphasized in three species which can be collectively called the proboscis anoles: *A. laevis* Cope, *A. phyllorhinus* Myers and Carvalho, and *A. proboscis* Peters and Orcés. The strange rostral appendages in these three anoles are probably confined to males; at least all known specimens of these species are males.

I here associate with this strange group of anoles, which lengthen the outline of the head by a swelling or soft protuberance, two undescribed species that elongate the bony frame of the snout itself. I associate these two with *punctatus* and its allies because of their general similarity in squamation despite the conspicuous difference in trend. This resemblance may be superficial and convergent, but I find the hypothesis of relationship useful as a provisional organization of the data. It is above all desirable at this moment to arrange and put in order the welter of *Anolis* species — even if somewhat artificially — and this is all the more desirable when still further species must be named.

The two species here described are, for South American species, remarkably distinct. It is usual in South American anoles to be uncertain whether a distinctive population is an unrecognized species or not. No such question exists in these cases. The first species I describe has such strong differences from all described species that I name it:

Anolis dissimilis new species

Holotype: CNHM[1] 81369, an adult ♂, Itahuania, upper Rio Madre de Dios, Madre de Dios Province, Peru, Kalinowski coll., 15 October 1954.

Diagnosis: Close to *Anolis proboscis* Peters and Orcés, *A. phyllorhinus* Myers and Carvalho, *A. laevis* (Cope), and *A. punctatus* Daudin. From all of these the new species differs by the absence of any trace of swelling on the snout, by having the ventrals in oblique rather than transverse rows, by its more slender body and longer, narrower head (measured to interparietal scale 1.5 times tibia, *ca.* ¼ snout-vent length).

Description. Head: All head scales wrinkled or striate, moderate to large posteriorly, small anteriorly. Seven scales across head

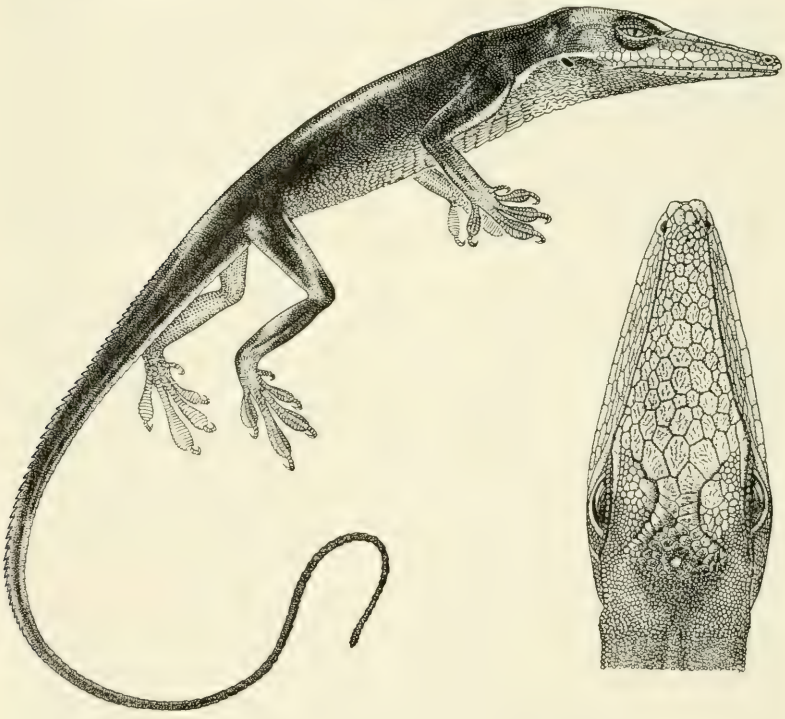

Fig. 1. *Anolis dissimilis* new species. Type, CNHM 81369.

[1]For abbreviations see p. 11.

between second canthals. No frontal ridges but a shallow frontal depression. Five scales bordering rostral posteriorly. Rostral partly divided. Nasal scale anterior to canthal ridge, separated from rostral by one scale. Six scales between supranasals.

Supraorbital semicircles broadly in contact, posteriorly partly separated from, anteriorly in contact with the supraocular disks, which consist of approximately nine enlarged scales, the anteromedial one much the largest, the remainder grading posteriorly into granules that become smaller toward the supraciliary margin, anteriorly grading more gradually into the moderately enlarged scales that are in contact with the single supraciliary. The latter short, continued posteriorly by undifferentiated granules, anteriorly fused on both sides with the first canthal. Canthus distinct, canthal scales nine, the second the longest, diminishing gradually forward. Loreal rows five, the lowest row distinctly the largest. Temporal and supratemporal scales subgranular, smooth, grading into the large flat but wrinkled scales that surround the interparietal. Interparietal very much larger than the very small ear, in contact with the supraorbital semicircles.

Suboculars in contact with supralabials, continued behind the eye by granules only, anteriorly in contact with the canthal ridge. Eleven supralabials to the center of the eye.

Mentals distinctly longer than wide, in contact with two elongate throat scales. Sublabials large, wide, four in contact with infralabials on one side, five on the other. Central throat scales elongate, swollen, not keeled.

Trunk: Middorsal scales feebly keeled, distinctly larger than flank granules but grading into them very gradually.

Ventrals larger than dorsals, swollen, smooth, subcycloid, imbricate or subimbricate, arranged in oblique rows.

Gular fan: Fan very large, extending well back on belly, scales narrow, smooth, much longer than ventrals, arranged in close-set lines.

Limbs and digits: Hand and foot scales multicarinate. Largest arm and leg scales unicarinate, smaller than ventrals. About 17 lamellae under phalanges 2 and 3 of fourth toe.

Tail: Tail distinctly compressed, surmounted by a crest of enlarged keeled scales, very uniform in size, that give it a very serrate upper border. Verticils not evident. Lateral caudal scales irregular in size, smaller. Ventral surface of tail covered by two rows of keeled, more elongate scales, smaller than crest scales.

Color: As preserved, essentially uniform dark above, lighter below. No evident pattern.

Size: Snout-vent length 56 mm.

The second species which requires description is most easily recognizable by a very narrow black line extending down the middle of the back. It is therefore described as:

Anolis nigrolineatus, new species

Holotype: MCZ 38940, Machala[1], El Oro Province, Ecuador. Luis A. Perez coll.

Paratype: USNM 12280, Guayaquil, Ecuador. No collector listed.

Diagnosis: Similar to *A. punctatus* Daudin but differing in color (lighter and with a black midvertebral line and faint dark markings on flanks and limbs) and in squamation (fewer scales in contact with the rostral, fewer lamellae under fourth toe).

Description. (Paratype differences in parentheses.) *Head:* Head scales moderate, posteriorly smooth, flat, anteriorly weakly keeled; 10 (8) scales across snout between second canthals; frontal depression distinct; 5 (7) scales border rostral posteriorly; anterior nasal scale in contact with rostral; 6 (5) scales between supranasals.

Supraorbital semicircles separated medially by 2 (1) scales from each other on each side and by one row of granules from the well-defined supraocular disk of 10–13 flat scales. One or two elongate supraciliaries bordered medially by polygonal scales and continued posteriorly by granules. Canthus indistinct anteriorly, *not* forming a single continuous row; 6 loreal rows, subequal.

Temporals and supratemporals both subgranular but the supratemporals longer and grading gradually into the somewhat enlarged scales surrounding the interparietal, which is larger than the ear and separated from the supraorbital semicircles by 3 to 4 scales. Scales posterior to interparietal grading very gradually into nape scales.

Suboculars weakly keeled, in contact with supralabials, anteriorly separated from canthal ridge by 4 (3) scales, posteriorly grading into temporals; 10–11 (8–9) supralabials to center of eye.

Mentals wider than long, deeply indented by first sublabials; 2–3 sublabials in contact with infralabials; 4 gular scales in a

[1]The exact locality of collection is in doubt. All specimens in the Perez collection come from El Oro Province and most from the vicinity of Machala but exact data were not kept. It would be preferable to make the USNM specimen the type of this very distinct species except that it is not as well preserved and the locality is not — with any probability — more exact.

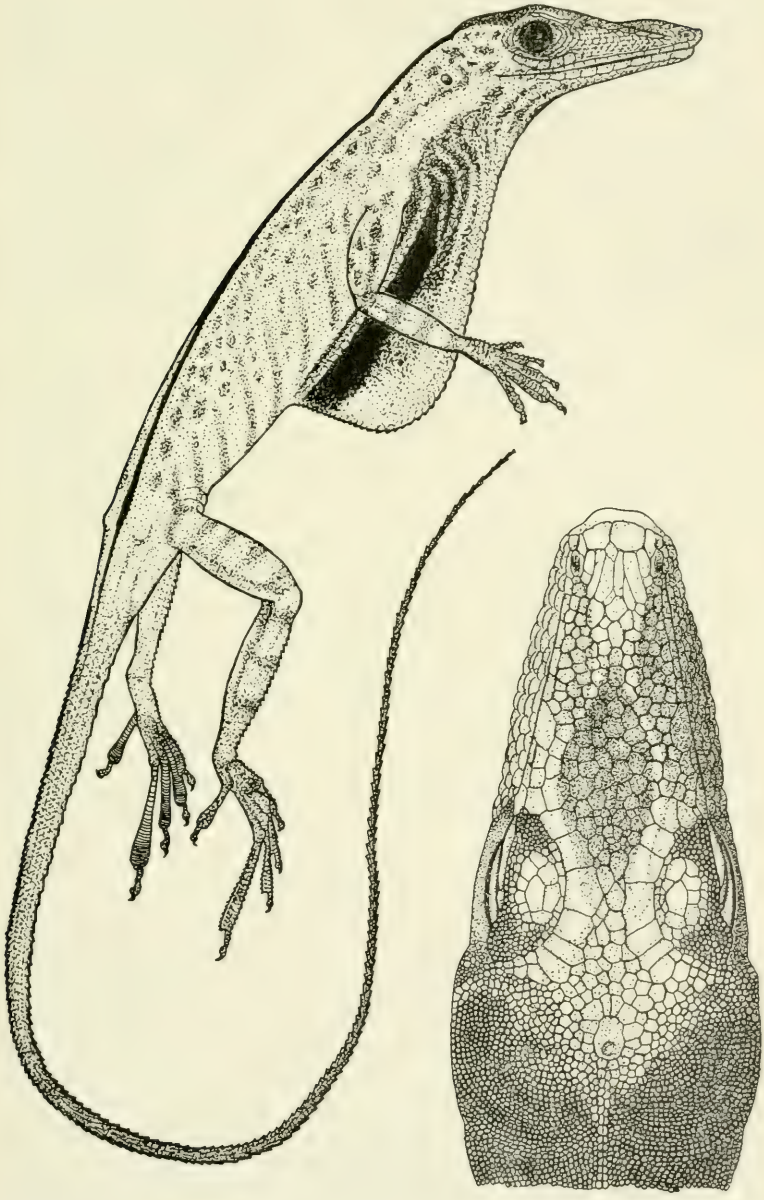

Fig. 2. *Anolis nigrolineatus* new species. Type, MCZ 38940.

gentle forward arc in contact with mentals between sublabials. Gular scales smallest medially grading laterally into sublabials.

Trunk: Two middorsal rows slightly but distinctly enlarged, swollen on nape, grading into flank granules. Ventrals larger, smooth, imbricate.

Gular fan: Very large, extending posteriorly onto more than the first third of the belly, rather densely scaled, the scales at the edge at least the size of the ventrals; smooth, lateral scales smaller.

Limbs: Scales on limbs unicarinate, the largest on hind limb larger than ventrals. Supradigital scales multicarinate. Eighteen lamellae under phalanges ii and iii of fourth toe.

Tail: Compressed, without verticils or dorsal crest. Greatly enlarged postanals present.

Color: As preserved, light brown with faint and broken streaking or reticulation. A black middorsal line two scales wide. Top of head including area around interparietal, but not supratemporals, blackish also. A dark postocular spot. Dewlap light at edge but with a *long* black spot at base.

Comparative material examined: A. punctatus (including the subspecies *boulengeri*): Specimens from many localities in Brasil, Bolivia, Peru, Ecuador and the Guianas.

A. laevis: Type only, ANSP 11368, between Moyabamba and Balsa Puerto on the Rio Huallaga, E. Peru.

A. phyllorhinus: [Type from Borba, lower Rio Madeira, Amazonas, Brasil, not seen], DZ 7118, Rio Tapajoz, Jacareacanga, Pará, Brasil.

A. proboscis: Type only, MCZ 54800, vicinity of Cunuco, N.W. of Mindo, on S. bank of Rio Mindo, Pichincha, Ecuador.

Definition of the *Anolis punctatus* species group

Reference of two new species to a "*punctatus*" group is an obligation to define the group. I attempt this after rather than before describing the new species because of the characteristic difficulties which attend all definitions of species groups within *Anolis* based on externals. This is a genus pervaded with convergence and parallel adaptation to such an extent that only those species series which are also obvious superspecies are clear, discrete units. Just beyond the level of the superspecies it is often not difficult to assemble larger clumps of species that seem evidently related. But here the problem of exclusion rather than inclusion enters. Each added species leads insensibly toward species still more remote from the core species of the putative group.

This situation is well exemplified by the *punctatus* group as here seen. A definition can be proposed but there will be multiple exceptions to certain characters, and certain fringe species which could as well be included or excluded.

A tentative definition (with exceptions) follows: Species of moderate size (but *nigrolineatus* is rather small, and *laevis* relatively large). The snout is produced either by bony structure, swelling, or soft proboscis. The color is probably green in life (usually purples and blues in alcohol), perhaps an exception in *nigrolineatus*. The ear is small and rather ventrally placed (on the level of mouth). The nostril is separated by a single prenasal scale from the rostral. The head scales are flat, pavimentose (even in *boulengeri*, which has keeled ventrals and keeling of the dorsal scales). The loreal rows are few (as few as two in *laevis*, as many as seven in *punctatus*. There are no or only a few scales between the supraorbital semicircles (0–2). The interparietal, larger than the ear, is of moderate size (large in *laevis*, *dissimilis* and *proboscis*) and separated from the semicircles by 0 to 4 scales. Suboculars broadly in contact with supralabials. Mental deep, not wide (widest in *nigrolineatus*). Well developed sublabials present. Dewlap large, scales in rows narrowly separated by naked skin (scales *not* in rows in *proboscis*). Middorsals not or not appreciably larger than flank scales (a dorsal crest in *proboscis*). Ventrals smooth (keeled in *boulengeri* which, however, intergrades with smooth-scaled *punctatus*), squarish, transverse. Tail more or less compressed with double row of scales dorsally (a single crest in *dissimilis* and *proboscis*).

This is an extensive list of similarities. However, the differences between species, emphasized above by the exceptions, are as striking as the similarities. They are of many sorts and it is natural to inquire whether the differences are less important than the common characters. It will be useful, therefore, to examine the differences in some detail.

1. *Snout differences.* *A. nigrolineatus* is in this regard not very different from many anoles not closely related to it: the bony structure of the snout itself has been stretched into a tapering, bluntly pointed structure. *A. dissimilis* carries the condition of *nigrolineatus* to an extreme. In contrast, the bony snout of *A. punctatus* is very little modified, but the rostral scale is swollen, protuberant. *A. laevis* has this scale produced into a broad-based flexible appendage. *A. phyllorhinus* has a narrow flexible appendage *above* the triangular rostral scale, this appendage having small granular scales. *A. proboscis* is very similar in the general conformation of the area but the scales on the flexible proboscis are

elongate. The differences here imply, as we have already suggested, that no single linear series can be envisioned; at least two are required. It is, however, possible to suppose that there has been radiation from a central type — perhaps *punctatus*, perhaps an ancestor of *punctatus*.

2. *Interparietal size.* The interparietal is large and in direct contact with the semicircles in so many species of diverse relationships, and the interparietal may so often differ in size and in distance from the semicircles in closely related species that this character is probably of minimal systematic value above the species or superspecies level.

3. *Dewlap squamation.* Again a character subject to much parallel modification and often different within a superspecies. *A. proboscis* is anomalous among the compared species in having a rather uniform squamation of the dewlap rather than scales in distinct, separated rows, but this is probably of no major significance.

4. *Dorsal crest. A. proboscis* is again very peculiar in having a dorsal crest of strongly enlarged sub-triangular scales. Such a crest is known in several West Indian so-called giant anoles but is very unusual in mainland species. It does, however, occur in some Guatemalan *A. pentaprion* — whether as an anomaly or a population character is unknown. Special though this feature seems in *A. proboscis*, it is hard to regard this as more significant than the extraordinary proboscis — so like that of *phyllorhinus* in which there is no hint of a dorsal crest.

5. *Tail.* The difference between a tail with two rows of scales dorsally and one with a pronounced single crest is a very obvious one. Schmidt (1939), in describing *Anolis barkeri*, and also Myers and Carvalho (1945), in describing *A. phyllorhinus*, have made much of the double-rowed condition — a feature which does appear to be unusual in anoles. There is usually in *Anolis* only a single row, whether or not this is produced into a crest. The systematic value of the double row is, however, much diminished by just the case in which Schmidt first used it: *A. barkeri* is a Mexican species which on osteological grounds (Etheridge, 1959) belongs to a very different section of the genus from the South American species in which this peculiarity is otherwise known.

In my judgment these differences, though disturbing at first glance, do not provide serious difficulty for a concept which unites all these species as a unit group. There are strong cross resemblances between species that on other characters would be separated. Thus, *dissimilis* shares with *proboscis* the character,

unusual in South America, of a crested tail, but in the nasal appendage and snout structure *proboscis* resembles *phyllorhinus* and is very different from *dissimilis*.

More awkward for the desiderate goal of taxonomic clarity are the species I have described as "fringe species." These are: *transversalis* (including *buckleyi*); the *solitarius-tigrinus* superspecies; *jacare*.

All of these have a double row of scales dorsally on the tail, all have smooth ventrals, few loreal rows, pavimentose dorsal head scales, few or no rows between the supraorbital semicircles, suboculars broadly in contact with supralabials, mental deep, not wide, well developed sublabials.

However, the ear is rather large, the color is complex with much cross-barring and spotting. The species of the *solitarius-tigrinus* series are all of small size (40–50 mm snout-vent length), *jacare* and *transversalis* are of moderate size. One peculiar feature which unites this set of species but is untrue or unknown for all those I have referred to the *punctatus* group (untrue for *punctatus*, unknown for the others) is the presence of black pigment in the female dewlap, and its absence in the male structure (which is also somewhat better developed).

To include these species in the *punctatus* group would seem to enlarge it too much; yet a considerable degree of affinity seems probable.

An evolutionary perspective for the *punctatus* group

The first described proboscis anoles — *A. laevis* Cope (Rio Huallaga, Peru) and *A. phyllorhinus* Myers and Carvalho (lower Rio Madeira, Brasil) were Amazonian. This is also true of *A. dissimilis* (on the upper Rio Madre de Dios). But *A. proboscis* Peters is from Pichincha Province in Ecuador, west of the Andean water shed, and *A. nigrolineatus* is from the Pacific lowlands near Guayaquil. *A. punctatus* — the central species of this putative complex — is much more widespread than any of the other species occurring in Amazonia, the Guianas and the forests of eastern Brasil, but neither it nor its western race (with keeled ventrals) — *boulengeri* — ever transgresses into the Trans-Andean Province.

There is, thus, in this species group — if it is a reality — no special geographic pattern except that of being clearly and wholly South American.

That this group is part of a wider autochthonous South American section of *Anolis* has been demonstrated by Richard Etheridge (1959). The species of the *punctatus* group, all examined radiographically by him, and a wider circle of forms which include such

species as *boettgeri*, *chloris*, *fasciatus*, *fraseri*, *frenatus*, *insignis*, *jacare*, *latifrons*, *microtus*, *mirus*, *nasofrontalis*, *peraccae*, *pseudotigrinus*, *solitarius*, *squamulatus*, *tigrinus*, *transversalis*, *ventrimaculatus*, are all characterized by possession of posterior caudal vertebrae without transverse processes and without autotomy septa, by the possession of four parasternal chevrons attached to the ribs and by having the lateral arms of the interclavicle divergent from the proximal parts of the clavicles. This is an assemblage of characters that Etheridge has demonstrated to be quite distinctive, and geographically quite coherent, occurring in species of mainland South America (but not those of the West Indies or Malpelo Island) and also in two or three species — *frenatus*, *insignis* and *microtus* — present in extreme southern Central America.

This is a very varied series in everything but these distinctive skeletal characters. These anoles are very different in size (including both dwarfs and giants), and in squamation (Table 2). The series, therefore, has every appearance of being an old assemblage which has had the time to diversify and which has exploited its opportunities.

The autochthonous South American section of *Anolis* shares South America with a group clearly not autochthonous but with its stronghold and center of origin to the north in Central America and Mexico. Though the latter group is clearly an invader from the north, it has reached every part of the total range of *Anolis* in South America. It is amazing that the ranges of these two groups of divergent history should be so closely coterminous in mainland South America.

This invader group is distinguished on Etheridge's osteological characters by having caudal vertebrae *with* caudal autotomy septa, *with* transverse processes which are inclined forward, and *with* an interclavicle the lateral arms of which are in contact with the clavicles. Osteologically, therefore, they are quite distinct from the old South American anoles. In squamation, as Table 2 shows, there is broad overlap. It is, therefore, impossible on external characters to make a separation of the two groups. Indeed, species belonging to the two groups have sometimes been confused with one another, and, in other cases, while the species characters permit ready separation, it will still be impossible *on externals* to allocate the species to group other than randomly.

Yet in bias and trend the two groups do differ. This too is shown in Table 2. In toe lamellae the bias of the alpha group is to higher numbers, that of the beta group to lower numbers. This character

(and probably more obscurely some of the others) is a reflection of an ecological bias in the two groups: the alpha group includes more deep forest, highly arboreal species, the beta group more species of open country — ground, grassland, or bush.

In ecology, as in so much else, there is strong overlap, but the bias or trend is clear. At the extreme of the beta series is an anole that actually lives in or at least takes refuge in holes in the ground (Ruthven, 1922), that in fact has abandoned wholly its arboreal heritage and with it the clinging hairs on the toe lamellae so characteristic of all other anoles. This anole, though only the extreme of its series, is customarily placed in a distinct genus; it is *Tropidodactylus onca*.

At the opposing extreme in the alpha series are probably to be placed the proboscis anoles — which again might be placed in a genus apart did they not seem to achieve their distinctive rostral structure in different ways. Neighbors to these in the extreme wing of the alpha series are *punctatus* and, if I interpret matters rightly, the two new species that are described in this paper.

Acknowledgments: I am deeply grateful to Dr. Gustavo Orcés-V. for allowing me to examine his Ecuadorian *Anolis* — material of extraordinary value — and for donating the type of *A. nigrolineatus* to the Museum of Comparative Zoology. Dr. Doris Cochran of the United States National Museum (USNM), Dr. Robert Inger of the Chicago Natural History Museum (CNHM), Dr. James E. Böhlke of the Academy of Natural Sciences, Philadelphia (ANSP), and Dr. Paulo Vanzolini, Departamento de Zoologia, Saõ Paulo (DZ) have generously allowed study of material under their care. James D. Lazell, Jr. prepared the figures of *A. nigrolineatus* and Nicholas Strekalovsky those of *A. dissimilis*. Dr. Mary Willson prepared the map. This series of studies on South American and other *Anolis* is supported by National Science Foundation Grant GB 2444.

LITERATURE CITED

Cope, E. D.
1875. Report on the reptiles brought by Professor James Orton from the middle upper Amazon and western Peru. Jour. Acad. Nat. Sci. Philadelphia, (2) 8: 159–188.

Etheridge, R.
1959. The relationships of the anoles (Reptilia: Sauria: Iguanidae): an interpretation based on skeletal morphology. University Microfilms, Ann Arbor. 236 pp.

Myers, G. S. and A. Carvalho
1945. A strange new leaf-nosed lizard of the genus *Anolis* from Amazonia. Bol. Mus. Nac., Rio de Janeiro, N. S. Zool., No. 43: 1–14.

Peters, J. A. and G. Orcés-V.
1956. A third leaf-nosed species of the lizard genus *Anolis* from South America. Breviora, No. 62: 1–8.

Schmidt, K. P.
1939. A new lizard from Mexico with a note on the genus *Norops*. Zool. Ser. Field Mus. Nat. Hist., **29**: 7–10.

Ruthven, A.
1922. The amphibians and reptiles of the Sierra Nevada de Santa Marta, Colombia. Misc. Publ. Mus. Zool. Univ. Michigan, **8**: 1–69.

(Received 26 July 1965.)

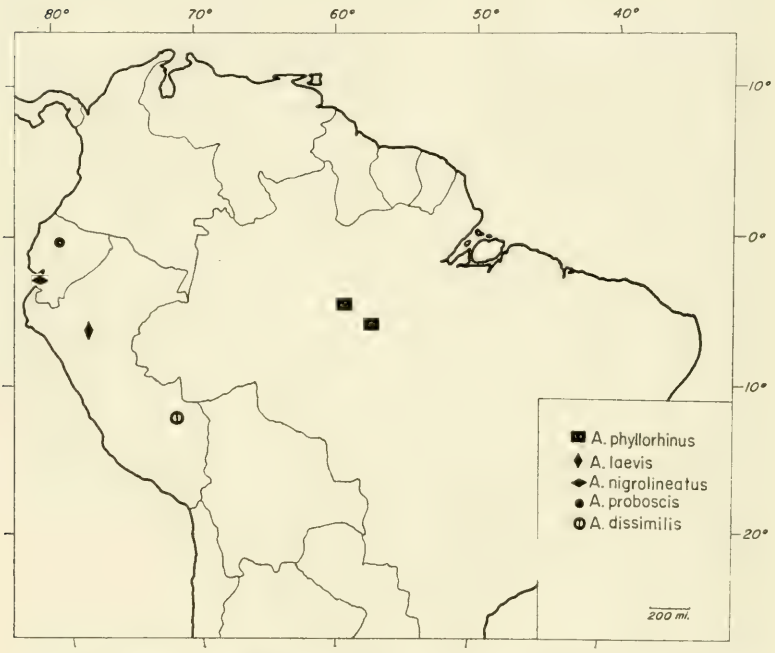

Fig. 3. Map of the distribution of *punctatus* group anoles except *A. punctatus* itself. The exact limits of the latter's very wide range are not known.

Table 1
Scale characters of *punctatus* group anoles

	punctatus Daudin 1802	*laevis* Cope 1875	*phyllorhinus* Myers & Carvalho 1945	*proboscis* Peters & Orcès 1956	*dissimilis* n. sp.	*nigrolineatus* n. sp.
proboscis	rostral swollen in ♂	soft protuberance covered with small scales (only ♂ known)	leaf-like, laterally compressed with granular scales (only ♂ known)	leaf-like, laterally compressed with elongate scales (only ♂ known)	no modification of snout (only ♂ known)	no modification of snout (only ♂ known)
scales between second canthals	11	4 (Cope)[1]	10	9	8	6
scales between semicircles	0 2	0	0	1	0	1–2
scales between interparietal and semicircles	2–4	0	1–2	2	0–1	3
temporals > or < dorsals	<	> (Cope)	=	<	<	=
loreals	4–7	2	4–5	4	4–5	5–7
suboculars in contact with supralabials	+	+	+	+	+	+
labials to center of eye	6–10	?	6–7	9	11	11

[1] Much of the information on *laevis* must come from Cope's original description. Although the type (ANSP 11368) is still in existence, it is in such poor condition that very little can be learned from it. However, the type confirms that there does exist a proboscis anole clearly different from those known by satisfactory material.

Table 1 — Continued
Scale characters of *punctatus* group anoles

	punctatus	*laevis*	*phyllorhinus*	*proboscis*	*dissimilis*	*nigrolineatus*
sublabials in contact with infralabials	2–7	?	5–6	2–3	2–4	2–3
median gular scales in contact with mental between sublabials	3–4	?	4	2	2	3–4
middorsal rows enlarged	0	0	0	1 (irregular crest)	gr	(gr)
tail crest	double row, no crest	double row, no crest	double row, no crest	+	+	double row, no crest
ventrals [1]	sti	stj	sti	sti	soj	st(i)
lamellae 4th toe	24–30	?	25–26	19	17	18
toe expansion	wide	narrow	wide	wide	wide	wide

[1] s = smooth; i = imbricate (i) subimbricate; j = juxtaposed; t = transverse; o = oblique; gr = middorsal enlarged, grading into flank scales.

Table 2

Character range in South American anoles

	alpha anoles	*beta anoles*
number of toe lamellae	14–30 (mode 18–21)	10-27 (mode 14–18)
scales across snout	4–25	7–20
scales between semicircles	0–5 (7 *)	0–4
dorsal scale rows enlarged	0–2	0–12

* Though several alphas range up to five scales between the supraorbital semicircles, the maximum reported here occurs in two exceptional specimens of *A. princeps* Boulenger (= ? *frenatus* Cope).

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STUDIES ON NEOTROPICAL POMPILIDAE (HYMENOPTERA)

I. THE GENUS *AGENIOIDEUS* ASHMEAD IN SOUTH AMERICA

BY HOWARD E. EVANS

The rich pompilid fauna of the neotropics has unfortunately been subjected to a good deal of bad taxonomy. The reasons are the usual ones: workers have been content to erect new species and genera without having seen the types of described species, which are widely scattered throughout Europe and North and South America; each worker has tended to use his own system of classification; and many parts of the neotropics remain very inadequately collected. The two papers of Nathan Banks on the South American Pompilidae [Bull. Mus. Comp. Zool., 96: 311–525 (1946), and 99: 371–486 (1947)] are useful, but suffer from all three of these deficiencies as well as from Banks' failure to cite references and his failure to cover quite a number of described species.

It will be many years before the taxonomy of the neotropical Pompilidae can be brought to a reasonably high level. In the meantime, I hope to publish a series of short papers covering such segments of the fauna as I am able to work out to my satisfaction. In addition to the specimens which Banks studied, I have seen much additional material from southeastern Brazil collected by Fritz Plaumann, several collections made in Chile and Peru by Luis Peña, and the material from a recent trip to Peru, Chile, and Argentina by C. C. Porter of Harvard University. I shall also make use of other material as available, including specimens from my own collecting in Mexico, Central America, and the West Indies. A review of the subfamily Pompilinae in Mexico and Central America is being published elsewhere (Mem. Amer. Ent. Soc., in press).

The genus *Agenioideus* is primarily characteristic of the warmer parts of the Holarctic region. There is considerable structural diversity within the genus, but the group nevertheless holds together well on the basis of wing venation, the weak development of the pulvillar pad and comb, and other features which I outlined in 1950 (Trans. Amer. Ent. Soc., 75: 189). One of the four North American species is confined to Mexico, two others range from southern United States into Mexico, and another (*humilis* Cresson) ranges all the way from southern Canada to Panama.

Banks did not regard *Agenioideus* as occurring in South America. However, three of the four species which he included in *Sericopompilus* do, in fact, belong in *Agenioideus*. The fourth species, *exilis* Banks, has only two submarginal cells and other features characteristic of the genus *Euplaniceps*, to which genus this species is here reassigned. To the best of my knowledge, *Sericopompilus* does not occur in South America. The three species of *Agenioideus* (which I regard as only two) are closely related and somewhat divergent from the North American *Agenioideus*, although still falling readily within that genus. Although the females lack a tarsal comb, as in the subgenus *Gymnochares*, the over-all resemblance is perhaps greatest to *Agenioideus sensu stricto*. A new subgenus, *Enbanksia*, is here proposed for this group. This group may represent the descendants of a stock of *Agenioideus* which succeeded in entering South America sometime during the Tertiary and which underwent a small radiation there.

A review of this small group seems justified at this time not only to clarify the correct generic position of these species, but also to properly characterize the male sex. Of the males assigned by Banks to South American *Sericopompilus*, only one (the allotype of *accoleus* Banks) properly belongs with this group. Also, Banks made several errors of fact which should be corrected; for example, he stated that the clypeus of the type of *accoleus* is "fully three and one-half times as broad as long" when in fact it measures 2.4 × as broad as long. He also did not have sufficient material to appreciate the variation in some of the characters used, for example in the dentition of the claws.

Enbanksia new subgenus

Type species. — *Sericopompilus accoleus* Banks, 1947.

Subgeneric characters. — Small wasps (4–9 mm), the females (and males of one species) with banded wings, both sexes with the tibial spurs entirely white and with a white spot near the base of the hind tibiae; males with the apical abdominal tergite white;

integument smooth and polished, except the front sometimes micropunctuate; body virtually without erect setae but extensively clothed with silvery pubescence, which is especially conspicuous on the posterior slope of the propodeum. Clypeus wider than lower face, truncate, with a slightly raised apical rim; antennae relatively short for the genus, third segment in the female not equal to the upper interocular distance, in the male not much if any longer than second segment; ocelli in a broad, flat triangle. Thoracic dorsum forming a rather smooth arc except the scutellum and metanotal disc prominent, somewhat compressed; pronotum sloping smoothly in front, its posterior margin broadly angulate or subangulate; postnotum somewhat polished, constricted on the midline; propodeal slope smooth and even; middle and hind tibiae strongly spinose, but the front tarsus without a comb, the apical tarsal segments not spined beneath. Claws dentate, the tooth sometimes close to the outer ray, such that the claws appear almost bifid; fore tarsal claws of male alike, both dentate. Wing venation similar to that of other *Agenioideus* (see Evans, 1950, Trans. Amer. Ent. Soc., 75: 190, fig. 58). Abdominal segments showing no strong tendency to telescope; male subgenital plate moderately compressed, simple (Figs. 3, 4); male genitalia without basal hooklets, but with some stout setae arising from a lobe at the base of the digitus (Figs. 1, 2).

Remarks. — This subgenus is named for N. Banks, who described all its presently known components.

KEY TO SPECIES AND SUBSPECIES

Females

1. Antennae short, third segment 2.0–3.5 × as long as thick, equal to .35–.45 × the upper interocular distance; wings with only one strong band, sometimes with a weak second band over the basal vein; legs beyond the basal part of the femora rufous.....1. *minutus* (Banks)
   Antennae longer, third segment 4.5–5.0 × as long as thick, equal to .65–.80 × the upper interocular distance; wings strongly twice-banded; legs fuscous, at least in large part 2

2. Pronotum and mesoscutum ferruginous, except the former with some pale yellow markings; front relatively narrow, middle interocular distance .56 × transfacial distance.....2a. *accoleus accoleus* (Banks)
   Pronotum and mesoscutum fuscous, except the former with pale yellow markings on the collar and often along the posterior margin; front broader, middle interocular distance .59–.61 × transfacial distance.....2b. *accoleus lucanus* (Banks)

Males

1. Wings clear hyaline, with a whitish bloom; legs rufous beyond basal parts of femora; third antennal segment wider than long; subgenital plate narrowly truncate apically (Fig. 3).....1. *minutus* (Banks)
   Wings banded; legs mostly fuscous; third antennal segment longer than wide; subgenital plate subacute apically (Fig. 4).....2

2. Pronotum, mesoscutum, scutellum, metanotum, and upper part of mesopleura ferruginous; middle interocular distance .59 × transfacial distance.....2a. *accoleus accoleus* (Banks)
   Thorax black; middle interocular distance .62–.66 × transfacial distance.....2b. *accoleus lucanus* (Banks)

1. Agenioideus (Enbanksia) minutus (Banks) new combination

Sericopompilus minutus Banks, 1947, Bull. Mus. Comp. Zool. Harvard, 99: 435. [Type: ♀, BRAZIL: Tres Lagoas, Matto Grosso, 6-10 Dec. (Cornell Univ. Exped.) (Cornell Univ.)]

Female. — Length 5.0–6.5 mm; fore wing 4.6–6.0 mm. Black, except as follows: pronotum with pale yellow markings on the collar and along the posterior margin; clypeus and mandibles rufo-testaceous, the latter darker apically; antennae rufo-testaceous except second and apical few segments usually somewhat infuscated; legs beyond the trochanters (or at least beyond the

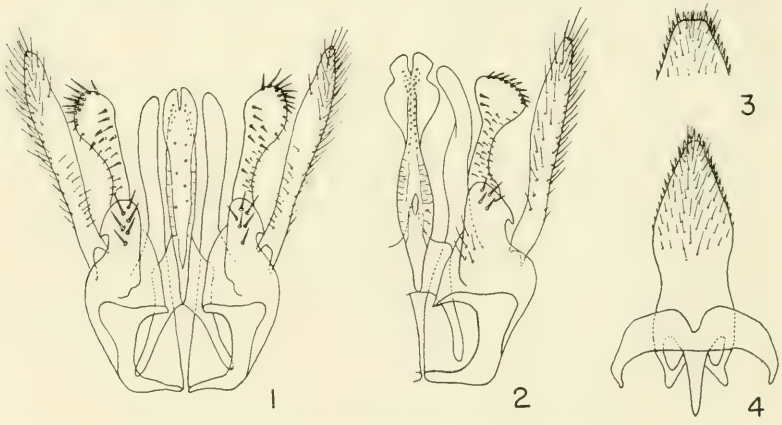

Fig. 1. Male genitalia of *Agenioideus* (*Enbanksia*) *minutus* (Banks), ventral aspect.
Fig. 2. Same of *A.*(*E.*) *accoleus lucanus* (Banks), left side omitted.
Fig. 3. Tip of subgenital plate of male *A.*(*E.*) *minutus* (Banks).
Fig. 4. Subgenital plate of male *A.*(*E.*) *accoleus lucanus* (Banks).

middle of the femora) bright rufo-castaneous; fore wings with a strong brown band from the marginal cell through the outer discoidal cell, some specimens weakly tinged with brown around the basal vein. Clypeus 2.9 × as wide as high. Front broad, middle interocular distance .65–.69 × transfacial distance; upper interocular distance .88–.94 × lower interocular distance; POL : OOL = 4:3. Third antennal segment three only slightly if at all longer than four, measuring 2.0–3.5 × as long as thick, .35–.45 × upper interocular distance. Propodeum somewhat more strongly convex and abdomen stouter than in the species which follows. All claws weakly dentate.

Male. — Length 5–6 mm; fore wing 4–5 mm. Black; pronotum marked with pale yellow on the collar and in a broad band along the posterior margin; coxae, trochanters, and basal parts of femora black, legs otherwise ferruginous except tarsi dusky; apical half of mandibles rufo-testaceous; antennae dark brown except scape pale beneath; wings clear hyaline, with a whitish bloom, veins and stigma brown. Clypeus 3 × as wide as high, truncate. Head broad, vertex forming a strong arc above the eye tops; front broad, middle interocular distance .67–.69 × transfacial distance; upper and lower interocular distances subequal, but middle interocular distance 1.2–1.3 × upper interocular distance; POL: OOL = 7:4. Third antennal segment very small, slightly wider than long, not longer than segment two or more than half the length of four. Postnotum slightly shorter than metanotum; propodeum in profile forming a somewhat higher arc than in the following species. Subgenital plate narrowly truncate apically (Fig. 3); genitalia as shown in Figure 1.

Distribution. — Southern Brazil, Paraguay, and eastern Peru.

Specimens examined. — 8 ♀♀, 3♂♂. BRAZIL: 7 ♀♀, 1 ♂, Nova Teutonia, Santa Catarina, Nov.–Feb. (F. Plaumann) [Mus. Comp. Zool., Cornell Univ., Coll. G. R. Ferguson]; 1 ♀, Tres Lagoas, Matto Grosso [type, Cornell Univ.]. PARAGUAY: 1 ♂, Caacupe, Oct. 25, 1955 (F. Schade) [Coll. G. R. Ferguson] PERU: 1 ♂, Avispas, Madre de Dios, 400 meters, Sept. 10–30 1962 (L. Peña) [Mus. Comp. Zool.].

2a. Agenioideus (Enbanksia) accoleus accoleus (Banks) new combination

Sericopompilus accoleus Banks, 1947, Bull. Mus. Comp. Zool. Harvard, 99: 433. [Type: ♀, BRAZIL: Maracajú, Matto Grosso, Apr.–May 1937 (G. Fairchild) (Mus. Comp. Zool.)]

Female. — Length 8.5 mm; fore wing 8.7 mm. Dark brownish-fuscous except as follows: mandibles and clypeus pale ferruginous, the latter with yellow blotching on each side; basal two antennal segments pale ferruginous, the remainder brownish; pronotum and mesoscutum ferruginous, except the collar marked with pale yellow and the posterior pronotal margin indistinctly marked with yellowish; front tibiae and tarsi testaceous; wings hyaline, fore wing with a strong brown band across the basal vein and a broader band across the wing at the marginal cell. Clypeus 2.4 × as wide as high. Front relatively narrow, middle interocular distance .56 × transfacial distance; upper interocular distance .80 × lower interocular distance; POL : OOL = 8:5. Third antennal segment 5 × as long as thick, .8 as long as the upper interocular distance. Slope of propodeum low and even, median line somewhat impressed. Claws strongly dentate, the inner ray acute, in the front tarsi the two rays rather close together, subparallel.

Male. — Length 7 mm; fore wing 6.5 mm. Dark brownish-fuscous except pronotal collar marked with pale yellow, remainder of pronotum ferruginous; mesoscutum, scutellum, metanotum, and upper two-thirds of the mesopleura also ferruginous; antennae brown except scape whitish below, flagellum testaceous below; legs brown except for the usual spot on the hind tibiae and the pale spurs; fore wings with a dark band at the marginal cell as in the female, but with only a weak, narrow infuscation at the basal vein. Clypeus 2.5 × as wide as high. Front rather narrow, middle interocular distance .59 × transfacial distance; upper interocular distance very slightly exceeding lower interocular; POL : OOL = 7:5; vertex weakly humped at the ocellar triangle. Third antennal segment rather short although longer than second, measuring about 1.2 × as long as thick. Postnotum nearly as long as metanotum; slope of propodeum very low and even. Terminalia as described under *accoleus lucanus*.

Distribution — Brazil (states of Matto Grosso and São Paulo).

Specimens examined. — Only the type and allotype, the latter from Campinas, São Paulo, March 1924 (F. X. Williams) [Mus. Comp. Zool.].

2b. Agenioideus (Enbanksia) accoleus lucanus (Banks) new status, new combination

Sericopompilus lucanus Banks, 1947, Bull. Mus. Comp. Zool., Harvard, 99: 434. [Type: ♀, BRAZIL: Nova Teutonia, Santa Catarina, 25 Jan. 1939 (F. Plaumann) (Mus. Comp. Zool.)]

Female. — Length 6.5–8.5 mm; fore wing 6.5–9.0 mm. Black, except as follows: mandibles and clypeus pale ferruginous, the latter sometimes with obscure yellowish blotching, sometimes infuscated on the upper half; basal 2.0–2.5 antennal segments testaceous; pronotum marked with pale yellow on the collar and usually with a more or less complete yellowish band along the posterior margin; legs fuscous, front tibiae and tarsi somewhat paler than the remainder; wings banded as in the nominate subspecies. Middle interocular distance .59–.61 × transfacial distance; upper interocular distance .82–.86 × lower interocular. Third antennal segment 4.5–5.0 × as long as thick, equal to .65–.75 × upper interocular distance. Claws of front tarsus variable, the inner ray close to the outer ray or somewhat removed from it. Other features as described for *a. accoleus.*

Male. — Length 6.0–6.5 mm; fore wing 5.0–5.5 mm. Dark brownish-fuscous except mouthparts and clypeus rufo-testaceous, basal two antennal segments and under side of segment three (and sometimes four) testaceous, front legs beyond the trochanters and also middle tibiae sometimes rufo-testaceous; wings banded as in female but the band over the basal vein weak. Middle interocular distance .62–.66 × transfacial distance; upper and lower interocular distances subequal. Third antennal segment 1.3–1.6 × as long as thick, sometimes barely shorter than fourth segment. Subgenital plate subacute apically (Fig. 4). Genitalia differing from those of *minutus* in having both the aedoeagus and the digiti more broadly expanded apically (Fig. 2).

Distribution — Southern Brazil (Santa Catarina).

Specimens examined. — 13 ♀ ♀, 4 ♂ ♂, all from Nova Teutonia, Santa Catarina, Oct.–March (F. Plaumann) [Mus. Comp. Zool., Coll. G. R. Ferguson].

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BREVIORA

Museum of Comparative Zoology

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A NEW SALAMANDER OF THE GENUS *CHIROPTEROTRITON* (CAUDATA: PLETHODONTIDAE) FROM MEXICO.

BY GEORGE B. RABB

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As Martin (1958:12) has noted, the karst caves of the Sierra Madre Oriental of Mexico are important amphibian habitats. Most of the salamander species found in such caves are widespread forms, but at least one described species from San Luis Potosí, *Chiropterotriton mosaueri*, is probably restricted to caves. Another species apparently in this category is described below. For it, I propose the name:

CHIROPTEROTRITON MAGNIPES sp. nov.

Figs. 1, 2

Holotype. — Museum of Comparative Zoology 30607, a young adult male collected in the Cueva de Potrerillos, about 2 km WSW of Ahuacatlán, which is approximately 8 km SW of Xilitla, San Luis Potosí, Mexico, on 18 November 1955 by Alejandro Villalobos F.

Paratypes. — MCZ 44033, CNHM 142457, and four uncatalogued specimens from the type locality in the collection of the Instituto Politecnico Nacional, Mexico, collected on 20 January 1952 by F. Bonet; UMMZ 125423 (GH 9878), collected at the type locality in July 1964 by Kraig Adler; CNHM 142458, UMMZ 125179, and three uncatalogued males in the Instituto Politecnico collection from Cueva del Madroño, near Laguna Colorada, Municipio de Landa de Matamoros, Querétaro, Mexico, collected on 16 January 1952 by F. Bonet.

Diagnosis — A species distinguished from all others in the genus by its very fully webbed feet, large size (adults 40–60 mm snout-vent length) and greater number of teeth (average of 79 maxillary-premaxillary in adult males).

Description of the holotype. — General habitus long and depressed. Tail relatively short (slightly less than snout-vent length), rounded in cross section. Basal constriction of tail not indicated. Limbs relatively long; adpressed limbs overlap by two or more costal spaces. Feet broad; toes and fingers joined by thick webbing. On foot, webbing indented between digits 2–3, 3–4, and 4–5 to level of distal end of penultimate phalanx of digits 3 and 4 (Fig. 1). Terminal pads, subtending digits 2–5 on foot and 2-4 on hand, present but not prominently developed, palmar surfaces of hand and foot otherwise smooth. Contours of digits not prominent dorsally, except for pigmentless areas marking some joints. Head flat and wide, eyes large and bulging. Prominent subocular groove extending in an arc from anterior corner of eye to position beneath posterior corner of eye. Postocular and other cephalic and nuchal grooves weakly developed. Viewed from above, snout truncate. Labial protuberances small. Total number of maxillary-premaxillary teeth 80; 64 countable mandibular teeth (dentary broken on left side near symphysis). Vomerine teeth in slightly arched single rows numbering 13 on each side. Teeth on posterior vomerine shelf beneath parasphenoid 93, arranged in two obovate patches slightly separated in midline. Skin rather thin. Mental gland not prominent, although marked by less pigment than rest of chin. Cloacal papillae well developed. Two symmetrical pockets with slit-like openings in dorsal posterior cloacal wall. Testis unilobate, pigmentless. Color of body in alcohol uniform dark lavender-brown above, somewhat lighter on ventral surfaces and feet. Palmar surfaces pigmentless. Post-iliac gland weakly indicated by light area. Anterior ends of ceratohyals blade-like, relatively narrow. Transverse processes of first caudal vertebra extend anteriorly to midpoint of preceding postsacral vertebra (see Fig. 2). Distal tarsal 5 large, articulating with fibulare and centrale 2–3; distal tarsal 4 accordingly not in contact with fibulare. Terminal phalanges with T-shaped distal ends. Measurements in mm, following techniques in Rabb (1958): Total length, 78; snout-vent length, 40.2; head width, 8.0; eye width, 3.2; nostril width, 0.4; snout-eye length, 1.8; snout-angle of jaw length, 7.1; arm length, 13.8; leg length 14.5; hind foot width, 6.5.

Variation. — The holotype is the smallest of the specimens studied. The others are variously shrunken by preservative, but the measurements are generally comparable (Table 1). Sexual dimorphism is apparent in the longer snout of the larger males, and perhaps in their relatively wider heads. Females evidently reach a larger size than the males, since three of the four available are

longer than the oldest and largest male. The tail is proportionately longer in males. The average number of vomerine and maxillary-premaxillary teeth is greater in the females, possibly reflecting the larger size and probably greater age of the females.

There is no marked difference detectable in the numbers of teeth in the three age classes represented among the males, although the high vomerine count of the largest male suggests a slight increase with age. The two larger males from Cueva de Potrerillos have some melanophores in the covering of the testes, but there is no such pigmentation in those from Cueva del Madroño. The number of glands in the mental cluster ranged from about 240 to 390 in the three males examined.

There is slight variation in the amount of webbing of the feet, but the average arrangement is that described for the type.

Habitat. — The type locality was well described by Bonet (1953). The cave is at an altitude of about 1300 m, and apparently in what was originally a cloud forest zone. According to the field notes of Dr. Villalobos, the topography of the cave in 1955 was considerably changed from that seen by Bonet in 1952.

Bonet (*op. cit.*) also provided data on the Cueva del Madroño, which is at an altitude of 1810 m in mixed pine-oak woods containing madroño (*Arbutus*) and *Carya*. The stalagmites in the cave were actively growing in 1952.

Judging from Bonet's account, *Chiropterotriton magnipes* was common in both the Cueva de Potrerillos and the Cueva del Madroño along with various cavernicolous arthropods. However, *C. magnipes* is not the only cave-inhabiting salamander in the region. A specimen collected by Dr. Villalobos at Cueva de la Hoya, which is only 3 km from the Cueva de Potrerillos, is referable to *C. arboreus* (MCZ 30605).

Relationships and comparisons. — The genus *Chiropterotriton* is composed of a group of Central American boletoglossal plethodontids that has a distinctive, relatively delicate, general habitus but few diagnostic characteristics. Taylor (1944) defined the group on the basis of the partial webbing of the feet. Tanner (1952) described the throat anatomy in various species, and Rabb (1956) described the skull and other anatomical features of the apparently most primitive species of the group. David Wake (*in litt.*) has informed me that the tarsal arrangement mentioned for *C. magnipes* distinguishes many members of the genus from the species groups in *Pseudoeurycea*. Although the foot shape is like that of certain species of *Bolitoglossa*, *C. magnipes* clearly belongs to the genus

Chiropterotriton in respect to general habitus, tarsal pattern, sublingual fold, form of the ceratohyal, and such features of its skeletal anatomy as can be determined from X-rays and one cleared and stained specimen (CNHM 142458). Wake and Brame (1963) indicated that fully-webbed conditions of the feet developed several times within the genus *Bolitoglossa*. The occurrence of a similar condition in a species of *Chiropterotriton* lends indirect support to their idea.

The feet of *Chiropterotriton magnipes* are unique in the genus in fullness of webbing and pad-like structure. The closest approach to the condition in *C. magnipes* is in an unnamed form from El Chihue, Tamaulipas (illustrated in Rabb, 1958, pl. II).

In proportions, *C. magnipes* differs from other *Chiropterotriton* in having a somewhat wider head (average, 19.1 per cent of snout-vent length in males). In relation to head length, *C. magnipes* has a large eye (average percentage, 35.5, ♂♂; 37.9, ♀♀), although the proportion is matched in *C. multidentatus* from Rancho del Cielo, Tamaulipas and El Chico, Hidalgo, and in the short-snouted species *C. bromeliacia*. In adults of most forms, this proportion is 29 to 33 per cent.

The tooth count averages in *C. magnipes* exceed the maxima for all other forms. However, the size of individual teeth in *C. magnipes* is small. The largest premaxillary teeth in males project about 0.25 mm from the gum, and the ordinary maxillary and dentary teeth are about half this size.

The foot structure and long limbs of *Chiropterotriton magnipes* indicate scansorial habits. The lack of testis pigmentation and the large eye suggest that the species is truly troglodytic and not a casual cave inhabitant. In these respects the species is slightly more specialized than the cave-dwelling *C. mosaueri* and the Tamaulipan *Chiropterotriton* with a large foot. Presumably its closest relationships are with these and other large, arboreal or scansorial northern Mexican species of the genus (*C. multidentatus*, *C. arboreus*).

Acknowledgements. — I am grateful to Dr. E. E. Williams for the opportunity to describe this salamander. Dr. Alejandro Villalobos F. of the Instituto de Biología, Universidad Autónoma de Mexico, has kindly supplied data on the type locality. Dr. F. Bonet of the Instituto Politecnico Nacional, Escuela Nacional de Ciencias Biologicas (IPN), loaned his series of *C. magnipes* for study and graciously allowed deposit of specimens in major U. S. collections. George Zug sent information on species in the University of Michigan Museum of Zoology (UMMZ). X-rays were made with

the beryllium-window machine at the University of Michigan by Kraig Adler. The prints are the work of Raymond Simpson. Abbreviations besides those indicated above are: MCZ, Museum of Comparative Zoology, and CNHM, Chicago Natural History Museum.

LITERATURE CITED

Bonet, F.

1953. Espeleologia Mexicana. Cuevas de la Sierra Madre Oriental en la region de Xilitla. Bol. Univ. Nac. Aut. Mexico Inst. Geol., **57**: vi+96 pp.

Martin, P. S.

1958. A biogeography of reptiles and amphibians in the Gomez Farias Region, Tamaulipas, Mexico. Misc. Publ. Mus. Zool. Univ. Michigan, **101**: 1–102, 7 pls.

Rabb, G. B.

1956. A new plethodontid salamander from Nuevo Leon, Mexico. Fieldiana: Zoology, **39**: 11–20.

1958. On certain Mexican salamanders of the plethodontid genus *Chiropterotriton*. Occ. Papers Mus. Zool. Univ. Michigan, No. 587: 1–37, 3 pls.

Tanner, W. W.

1952. A comparative study of the throat musculature of the Plethodontidae of Mexico and Central America. Univ. Kansas Sci. Bull., **34**: 583–677.

Taylor, E. H.

1944. The genera of plethodont salamanders in Mexico. Pt. I. Univ. Kansas Sci. Bull., **30**: 189–232.

Wake, D. B. and A. H. Brame, Jr.

1963. The status of the plethodontid salamander genera *Bolitoglossa* and *Magnadigita*. Copeia, 1963: 382–387.

TABLE 1
Quantitative data on the type series of *Chiropterotriton magnipes*[1]

	Cueva de Potrerillos							Cueva del Madroño				
	MCZ 30607 ♂1	MCZ 44033 ♂2	CNHM 142457 ♀	IPN ♀	IPN ♀	IPN ♀	IPN ♂1	CNHM 142458 ♂3	UMMZ 125179 ♂2	IPN ♂1	IPN ♂1	IPN ♂2
Snout-vent length (mm)	40.2	53.1	59.0	59.0	60.0	51.8	47.1	55.2	50.0	51.6	54.6	48.2
Tail length (mm)	37.8	58.6	60.0	64.2	51+	53.0	36+	65	53.6	66.6	62.2	68
Snout to jaw/snout to vent (%)	17.66	20.72	16.78	17.80	18.00	17.76	19.32	19.20	21.40	20.16	19.41	21.37
Head width/snout-vent length	19.90	19.02	17.96	18.14	17.67	19.50	18.47	18.30	19.80	18.80	18.86	19.71
Snout to eye/snout to jaw	25.53	34.25	30.77	33.33	31.94	34.43	35.00	38.57	36.62	39.13	38.57	36.76
Snout to eye/head width	22.64	37.31	28.57	32.39	32.86	31.43	36.21	40.30	40.00	42.19	39.71	39.68
Number of vomerine teeth	26	26	28	42	50	33	26	41	23	32	26	36
Number of maxillary-premaxillary teeth	80	75	78	63+	119	84	74	83	77	77	76	91
Number of dentary teeth	64	67	62	83	114	93	76	100	100	84	103	110

[1] Instituto Politecnico specimens were uncatalogued.
Numerals after male symbols indicate number of testis lobes.
Plus symbol indicates incomplete count or broken tail.

Fig. 1. *Chiropterotriton magnipes* sp. nov., holotype MCZ 30607. × 2.1.

Fig. 2. Radiograph of *Chiropterotriton magnipes*, UMMZ 125423 (GH 9878), an adult female. Right maxilla is broken. Arthropods in the gut obscure body vertebrae. $\times 1.25$.

BREVIORA

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VARIATION IN THE NUMBER OF MARGINAL TOOTH POSITIONS IN THREE SPECIES OF IGUANID LIZARDS

BY

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Although tooth counts (more accurately, the number of tooth positions) are customarily given in the description of fossil lizards, their possible taxonomic value is generally unassessable for want of quantitative data on adequate samples of modern lizards. Further, the possible developmental and adaptive implications of tooth number have been inadequately explored. Edmund (1960, p. 66) notes an apparent lack of correlation between wave length in tooth replacement and number of tooth positions in iguanids, but the condition in juveniles of species with long wave lengths, such as *Ctenosaura pectinata* with 11 teeth per wave, would be especially interesting. Hotton (1955, p. 97) in a study of adaptive relations of dentition to diet in iguanids, including *C. similis*, states regarding tooth number only that there are "slight tendencies toward fewer teeth in the maxillary row . . . in smaller individuals."

The availability of adequate, though not impeccable, samples of cranial material (assembled for other purposes) representing *Ctenosaura similis*, *C. pectinata*, and *Anolis carolinensis* suggested the desirability of characterizing these samples statistically, in order to compare ontogenetic and taxonomic variability in number of tooth positions, and strength of correlation between number of tooth positions and length of tooth row among two closely related taxa and one distantly related taxon.

MATERIAL

Ctenosaura similis: Well-preserved, dissociated elements representing no less than 223 individuals, collected from deposits in the ruins of Mayapan (20°37′48″N, 89°27′42″E), Yucatan, during expeditions (1950–1956) of the Department of Archaeology, Carnegie Institution of Washington. Among the more than 6000 bones identified from these deposits, over a third pertain to *C. similis*, the only lizard represented (Pollock and Ray, 1957). The material utilized in the present study undoubtedly dates almost entirely from the period of major occupation of the city, the Maya Resurgence, estimated (and in part confirmed through radiocarbon dating) to have extended from about 1200 through 1450 A.D. Thus the sample was accumulated during an interval of perhaps 250 years or more. The specimens probably were secured within close proximity of the city. The sample is undoubtedly biased in favor of large individuals. Early juveniles are absent altogether. Although there is certainly high representation of left and right sides of single individuals among the dissociated maxillae and dentaries, the correspondence is far from complete and can be demonstrated in no given instance. The material was made available for study and was deposited in the Museum of Comparative Zoology at Harvard College through the courtesy of Dr. H. E. D. Pollock.

Ctenosaura pectinata: Cleaned skulls of 17 modern specimens collected over many years at widespread localities through the range of this nominal species. Specimens are housed in the collections of the Museum of Comparative Zoology, American Museum of Natural History, Chicago Natural History Museum, and University of Michigan Museum of Zoology, and were made available by the curators of those collections.

Anolis carolinensis: Macerated skulls of 58 individuals collected during 1955 in the vicinity of Gainesville, Alachua County, Florida. This sample, like those of *Ctenosaura*, does not include very young individuals, and thus is not ideal for the study of growth phenomena. In other respects it is for statistical purposes the most desirably constituted sample of the three. The specimens were made available by Dr. Walter Auffenberg and are deposited in the Museum of Comparative Zoology.

METHODS

The following symbols represent the statistics calculated in this study:

N = the number of individuals in the sample.

$\bar{x}$ = the mean of x, here the straight-line length of tooth row, maxillary or dentary.
$\bar{y}$ = the mean of y, here the number of teeth or tooth positions per maxilla, dentary, or premaxilla (fused premaxillae).
s_x = the standard deviation of x.
s_y = the standard deviation of y.
V_x = the coefficient of variation of x.
V_y = the coefficient of variation of y.
OR_x = the observed range of x.
OR_y = the observed range of y.
r = the coefficient of correlation, here between x and y.
a = the growth ratio.
σ_a = the standard error of a.
b = the initial growth index.
s_d = the standard deviation of the diagonal distances of points from the reduced major axis; a measure of absolute dispersion of points about that axis.
D_d = the coefficient of relative dispersion about the reduced major axis.
z = statistic computed in testing for significant difference in slope of growth lines.

Most of these are the familiar statistics of univariate and bivariate analysis dealt with in standard statistical handbooks. However, Imbrie's paper (1956) is especially valuable regarding the basis for utilization of the reduced major axis rather than regression lines, as well as for a lucid interpretation of all of the statistics used herein.

Premaxillae: The fused premaxillae were treated as a single median element. Only the number of tooth positions was determined for this element, as adequate means of measuring the (short) length of the tooth row, especially in *Anolis*, were not at hand when the samples were assembled. Thus only the standard univariate statistics are presented (Table 1, Figure 1).

Maxillae and dentaries: All of the statistics listed above were computed for both left and right maxillae and dentaries of the two samples of *Ctenosaura*, and for the right side only of *Anolis* (Tables 2, 3, and 4). As a check on symmetry, the frequency distribution for length of tooth row and number of tooth positions was in every case represented by histograms, one example of which is presented here (Fig. 2). Scatter diagrams of the two variates were prepared in each case, from which it was determined that the distribution of points approximates a straight line closely enough to

permit representation of the growth line by the equation: $y = ax + b$. The scatter diagrams for all elements of the right side are presented in Figures 3 and 4.

RESULTS

Premaxillae: As might be anticipated, the two species of *Ctenosaura* are very similar, in fact essentially identical, in statistical characteristics of tooth number, and differ considerably from *Anolis carolinensis* (Table 1). Actually, these representatives of the two genera differ much more strikingly than the statistics alone reveal. For practical purposes it can be said that the variate will never assume an odd value in *Anolis*[1], whereas it does so in 70 per cent or more of the *Ctenosaura* sampled (Fig. 1). The tooth count in an *Anolis* premaxilla more likely than not will be 10, and in *Ctenosaura* 7. The fact that premaxillary tooth counts in *Anolis* can assume only even values might suggest that the coefficient of variation (V_y) for *Anolis* is artificially high. However, if only one side of the fused element is considered, with tooth counts of 3–6, V_y is not altered. The V for tooth counts here and in the maxillae and dentaries is of little interest except that it reflects rather low variation in tooth number over the broad size range represented in the samples.

Maxillae and dentaries: The frequency distribution for number of tooth positions is in general approximately symmetrical (Fig. 2B), although it is skewed considerably to the right in the right dentary of *Anolis*. The length of tooth row in no case approaches a normal curve, and a polymodal frequency distribution is suggested for *Ctenosaura similis* (Fig. 2A) and *Anolis*, particularly the former; N is not adequate to suggest a pattern in *C. pectinata*. It is tempting to suppose that broadly overlapping frequency distributions of different sexual or age classes or both are responsible for the polymodality, analogous to that demonstrated by Klauber (1937, fig. 4) for *Crotalus v. viridis*, but this could not be tested on the basis of samples at hand.

The number of tooth positions per se is not very useful in distinguishing the three taxa tested. It is of no value in separating the two species of *Ctenosaura*, and its power of resolution is very low even between taxa as remote as *Ctenosaura* and *Anolis*. Tooth

[1] Reference to "*Anolis*" and to "*Ctenosaura*" is to be understood as a shorthand device applying only to the samples tested here, and in no case to either genus as a whole.

count alone in an isolated fossil specimen would be of taxonomic interest only if it lay within the portion of the *Ctenosaura* distribution well above the OR of *Anolis*. The sample of *Anolis* is separable from those of *Ctenosaura* on the basis of absolute length of toothrow, which reflects the valid biological distinction that *Ctenosaura* is a much larger lizard, although the true population parameters unquestionably overlap. The two samples of *Ctenosaura* are not clearly distinguishable on the basis of any statistic presented in Tables 3 and 4. The relatively high values of V_x, V_y, s_d, and D_d in *Ctenosaura pectinata* reflect principally its greater OR_x but may result in part also from geographic variation, not a factor in the other two samples.

The most interesting features of the relation between length of tooth row and number of tooth positions in the samples studied are the relative strength of correlation between the two variates and the slope of their growth line[2]. The two samples of *Ctenosaura* are essentially identical in these features. Both samples exhibit a strong correlation between the variates, both visually (Figs. 3A, B, and 4A, B) and statistically (minimum value of r = .83). The probability is greater than .05 that the minor deviations in slope of the growth lines are attributable to chance, for the values of z are in every case less than 1.96 (Table 4).

Anolis, on the other hand, differs radically from *Ctenosaura* both in strength of correlation and in slope of growth line. Correlation is not visually detectable (except in a mildly suggestive linear clustering of points within the wide scatter) in Figures 3C and 4C, and is only weakly indicated by the correlation coefficient. However, the probability of obtaining a calculated r as great as .24 if the sample was drawn from a population in which $\rho = 0$ is less than .10, or, if, as is reasonable on developmental grounds, it is assumed that r is necessarily positive, less than .05 (Simpson, Roe, and Lewontin, 1960, appendix table V, p. 426). The slope of the growth line is very steep in *Anolis*, very gentle in *Ctenosaura*. The difference in slope is statistically highly significant (Table 4), but biologically means only that the teeth of *Anolis* are considerably smaller than those of *Ctenosaura*. Thus, more teeth per unit increase in length of tooth row can be accommodated in *Anolis* than in *Ctenosaura*.

[2] Strictly speaking, the line is not purely a "growth" line as the scatter of points on which it is based undoubtedly represents in part non-ontogenetic variation. Designation of the line as a growth line rests on the assumption that regression in individuals of different sizes is the same as in individuals of different ages.

Although so few samples provide the basis for no more than suggested interpretations, it may be supposed that a difference such as that observed in correlation between number of tooth positions and length of tooth row has adaptive significance. The most fundamental adaptive distinction relating to dentition between *Anolis* and *Ctenosaura* is in diet; *Anolis* is a predatory insect eater, and *Ctenosaura* an extreme vegetarian. In *Ctenosaura* the maxillary and dentary tooth rows constitute continuous dental palisades in which the broadly expanded, strongly cusped crowns (more pronounced posteriorly) succeed one another in close order, and tend to overlap, an arrangement apparently advantageous in leaf-chopping, whereas in *Anolis* the tooth rows constitute open series in which the broadly based, apically narrow teeth with weak cusps are separated by variable gaps, possibly adaptive in the apprehension and puncturing of insect prey (Fig. 5). If in a strict vegetarian there is selective advantage in maintaining a continuous tooth row, it would be reasonable to expect a consistent addition of tooth positions with increasing size, i.e., a strong positive correlation between the two phenomena. The slope of the growth line would depend in part on the size of additional teeth and on the degree of increase in size of successive replacement teeth. In a form such as *Anolis carolinensis* with no apparent selection pressure toward a closed tooth row, and perhaps with positive selection for an open tooth row, one might expect only a loose correlation between number of tooth positions and length of tooth row. Obviously these suggestions require testing on broader ontogenetic series of the taxa studied, and on similar series of other taxa.

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LITERATURE CITED

Edmund, A. G.
1960. Tooth replacement phenomena in the lower vertebrates. Roy. Ontario Mus., Life Sci. Div., Contrib. No. 52: 1–190, 58 figs.

Hotton, Nicholas, III
1955. A survey of adaptive relationships of dentition to diet in the North American Iguanidae. Am. Midland Nat., **53**: 88–114.

Imbrie, John
1956. Biometrical methods in the study of invertebrate fossils. Bull. Am. Mus. Nat. Hist., **108**: 211–252, 10 figs.

Klauber, L. M.
1937. A statistical study of the rattlesnakes. IV. The growth of the rattlesnake. Occ. Pap. San Diego Soc. Nat. Hist., **3**: 1–56, 6 figs.

Pollock, H. E. D., and C. E. Ray
1957. Notes on vertebrate animal remains from Mayapan. Carnegie Inst. Washington, Dept. Archaeol., Current Repts., **41**: 633–656.
Simpson, G. G., Anne Roe, and R. C. Lewontin
1960. Quantitative zoology. Harcourt, Brace and Co., New York, vii + 440 pp., rev. ed.

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Table 1. Univariate statistical characterization of tooth count (y) in the fused premaxillae of three iguanid lizards.

Statistic	*Ctenosaura similis*	*Ctenosaura pectinata*	*Anolis carolinensis*
N	74	17	58
$\bar{y}$	7.05 ± .07	7.18 ± .17	9.72 ± .21
s_y	.63 ± .05	.70 ± .12	1.60 ± .15
V_y	8.94 ± .73	9.75 ± 1.67	16.40 ± 1.52
OR_y	6–9	6–9	6–12

Table 2. Bivariate statistical characterization of length of tooth row (x) and tooth count (y) in the maxillae of three iguanid lizards.

Statistic	*Ctenosaura similis* Left	*Ctenosaura similis* Right	*Ctenosaura pectinata* Left	*Ctenosaura pectinata* Right	*Anolis carolinensis* Right
N	79	60	17	17	58
$\bar{x}$	31.68 ± .81	32.94 ± 1.00	31.31 ± 2.13	31.61 ± 2.17	7.64 ± .16
$\bar{y}$	24.77 ± .27	25.27 ± .31	23.29 ± .60	23.82 ± .65	18.26 ± .20
s_x	7.18 ± .57	7.52 ± .69	8.79 ± 1.51	8.96 ± 1.54	1.22 ± .11
s_y	2.36 ± .19	2.43 ± .22	2.49 ± .43	2.66 ± .46	1.49 ± .14
V_x	22.66 ± 1.80	22.83 ± 2.08	28.07 ± 4.81	28.35 ± 4.86	15.97 ± 1.48
V_y	9.53 ± .76	9.62 ± .88	10.69 ± 1.83	11.17 ± 1.92	8.16 ± .76
OR_x	17.4 − 44.6	15.9 − 44.8	14.5 − 42.9	15.4 − 45.5	5.5 − 10.0
OR_y	19–30	17–31	18–27	19–29	15–22
r	.85	.88	.85	.84	.29
a	.329	.323	.283	.30	1.22
σ_a	.020	.020	.036	.040	.153
b	13.34	14.63	14.43	14.34	8.94
s_d	4.14	3.87	5.00	5.29	2.29
D_d	10.29	9.33	12.82	13.36	11.59

Table 3. Bivariate statistical characterization of length of tooth row (x) and tooth count (y) in the dentaries of three iguanid lizards.

Statistic	*Ctenosaura similis*		*Ctenosaura pectinata*		*Anolis carolinensis*
	Left	Right	Left	Right	Right
N	129	138	17	17	58
$\bar{x}$	36.41 ± .73	36.19 ± .62	33.66 ± 2.35	34.05 ± 2.26	8.18 ± .15
$\bar{y}$	31.44 ± .29	31.49 ± .26	28.76 ± 1.10	29.29 ± 1.07	22.62 ± .19
s_x	8.25 ± .51	7.33 ± .44	9.68 ± 1.66	9.30 ± 1.60	1.12 ± .10
s_y	3.25 ± .20	3.05 ± .18	4.54 ± .78	4.42 ± .76	1.44 ± .13
V_x	22.66 ± 1.41	20.25 ± 1.22	28.76 ± 4.93	27.31 ± 4.68	13.69 ± 1.27
V_y	10.34 ± .64	9.69 ± .58	15.79 ± 2.71	15.09 ± 2.59	6.37 ± .59
OR_x	20.3 – 53.3	20.0 – 48.8	16.2 – 48.3	16.5 – 48.4	6.0 – 10.0
OR_y	24–42	23–39	21–36	20–36	19–25
r	.87	.83	.87	.88	.24
a	.394	.416	.469	.475	1.29
σ_a	.017	.020	.056	.055	.164
b	17.10	16.43	12.97	13.12	12.07
s_d	4.52	4.63	5.45	5.04	2.25
D_d	9.40	9.65	12.31	11.23	9.35

Table 4. Values of the statistic z in tests for significant difference in slope of pairs of growth lines.

	Maxilla	Dentary
C. similis		
left - right	.22	− .84
C. pectinata		
left - right	− .317	− .08
C. similis - *C. pectinata*		
left - left	1.12	− 1.28
right - right	.52	− 1.02
C. similis - *Anolis*		
right - right	5.83	5.28
C. pectinata - *Anolis*		
right - right	5.82	4.70

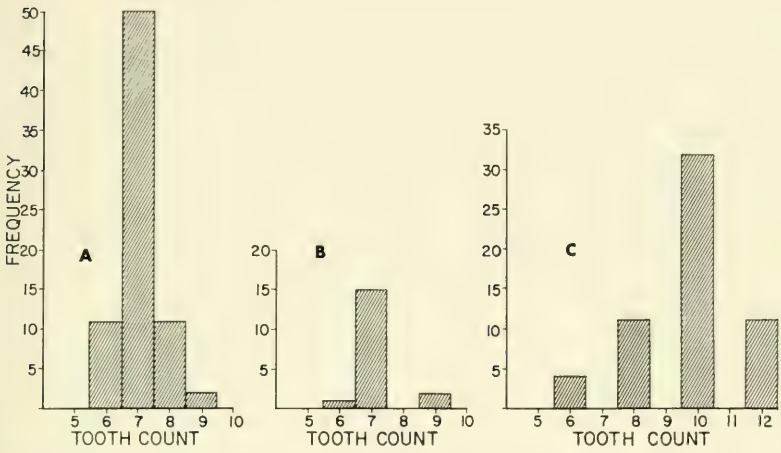

Fig. 1. Histograms illustrating the frequency distribution of tooth counts in the fused premaxillae of (A) *Ctenosaura similis*, (B) *C. pectinata*, and (C) *Anolis carolinensis*.

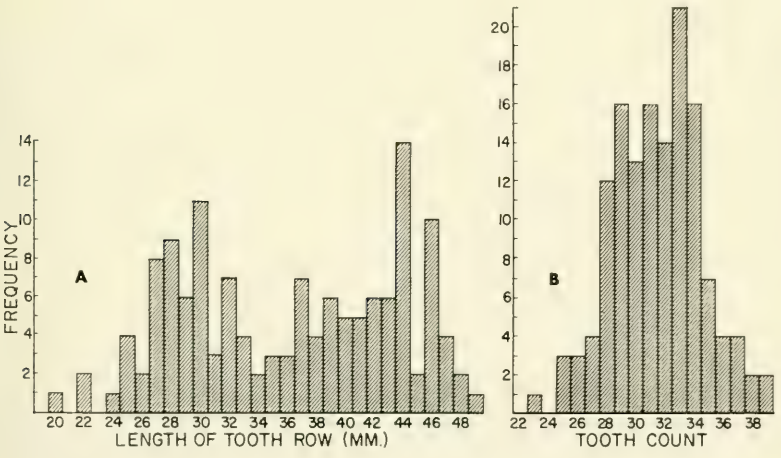

Fig. 2. Histograms illustrating the frequency distribution of (A) length of tooth row and (B) tooth counts in the right dentary of *Ctenosaura similis*.

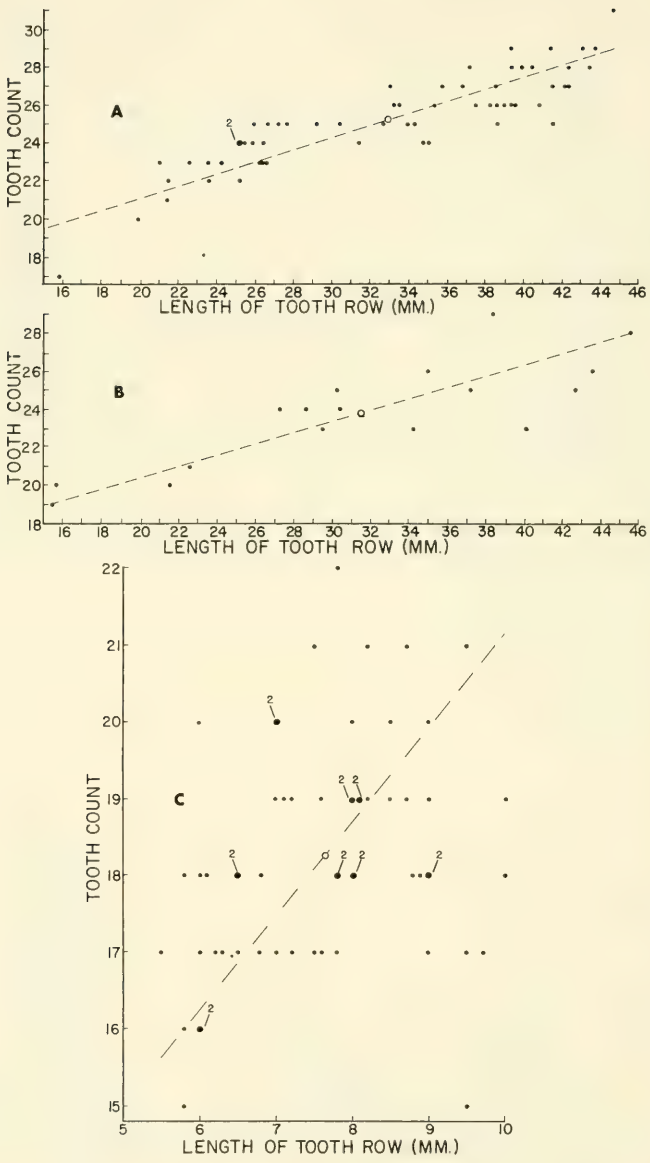

Fig. 3. Scatter diagrams showing tooth counts (y) and length of tooth row (x) in the right maxillae of (A) *Ctenosaura similis*, (B) *C. pectinata*, and (C) *Anolis carolinensis*. The broken line represents the reduced major axis; the open circle, the joint mean.

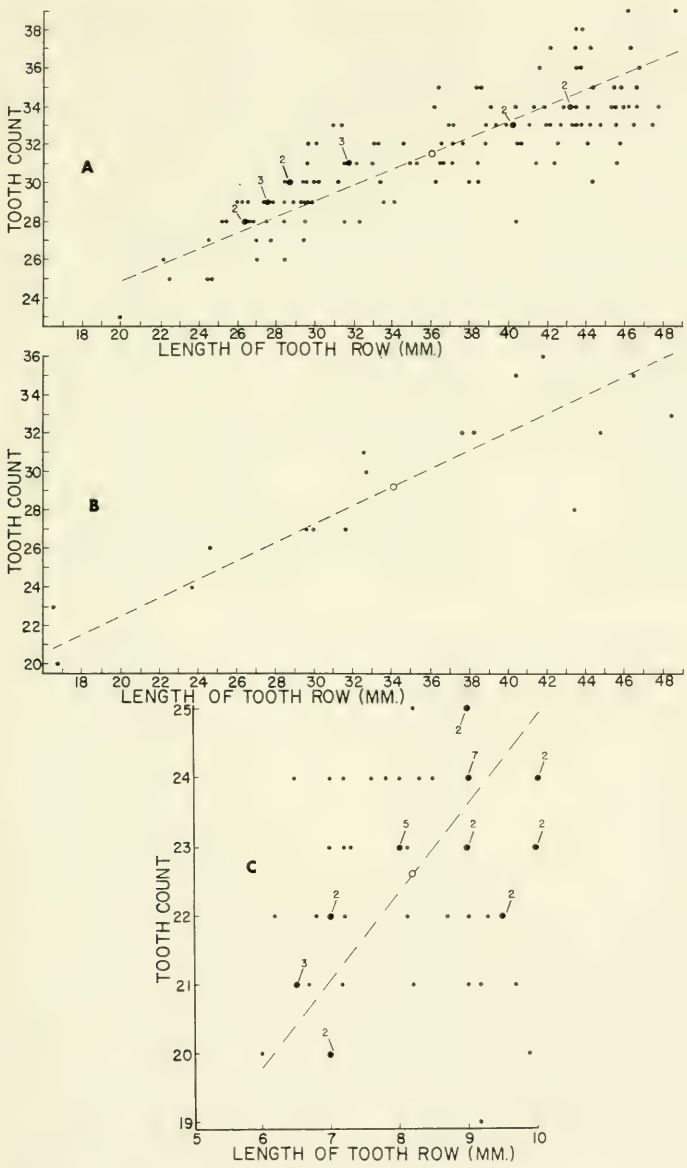

Fig. 4. Scatter diagrams showing tooth counts (y) and length of tooth row (x) in the right dentaries of (A) *Ctenosaura similis*, (B) *C. pectinata*, and (C) *Anolis carolinensis*. The broken line represents the reduced major axis; the open circle, the joint mean.

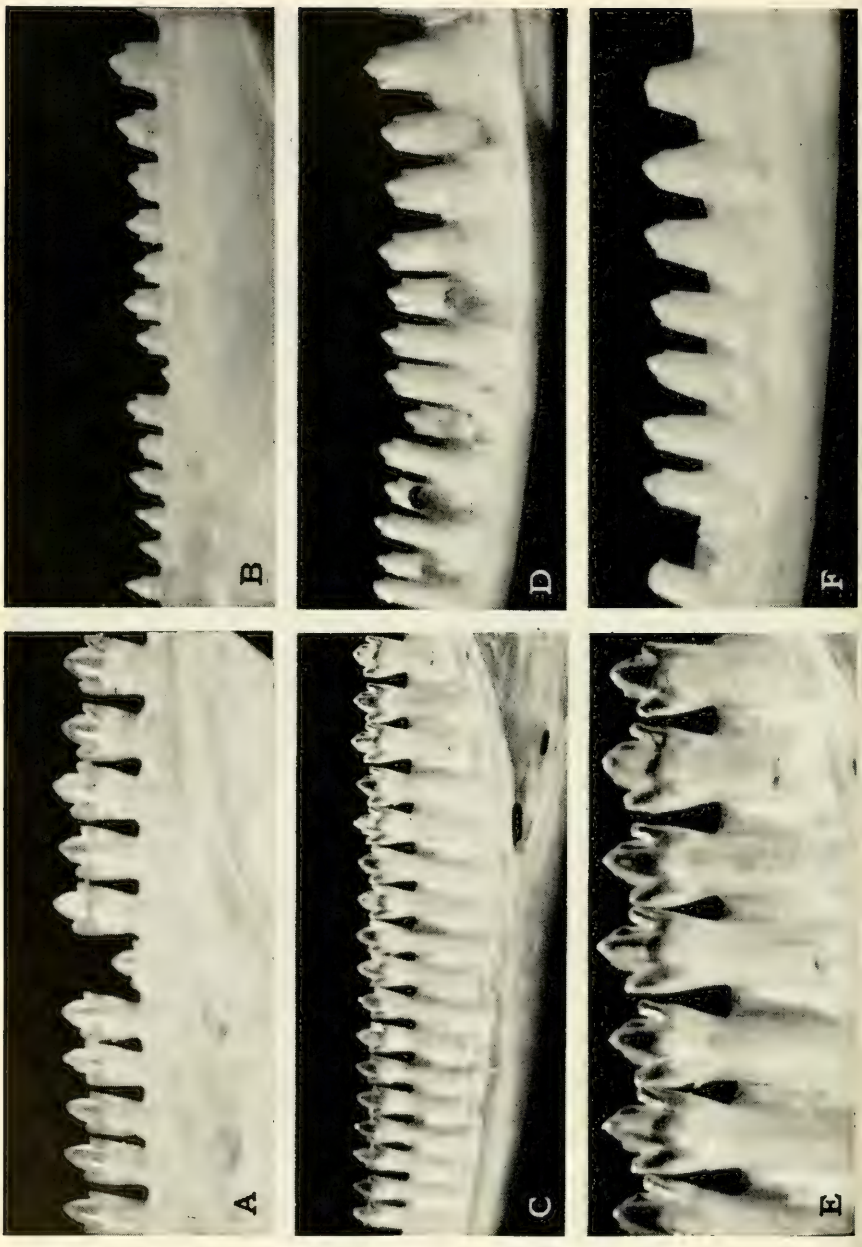
A
B
C
D
E
F

Fig. 5. Dentitions of *Ctenosaura* and *Anolis*: (A) *C. similis*, MCZ 36802, partial right maxillary tooth row in labial aspect, (B) *A. carolinensis*, MCZ 57382b, partial right maxillary tooth row in labial aspect, (C) *C. similis*, MCZ 36802, partial right dentary tooth row in lingual aspect, (D) *A. carolinensis*, MCZ 57382x, partial right dentary tooth row in lingual aspect, (E) *C. similis*, MCZ 36802, posterior portion of right dentary tooth row in lingual aspect, (F) *A. carolinensis*, MCZ 57382j, posterior portion of right dentary tooth row in lingual aspect. Scale varied, 5 15 ×.

BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. DECEMBER 15, 1965 NUMBER 237

A NEW SPECIES OF THE ANT GENUS *DACETINOPS* FROM SARAWAK[1]

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The singular myrmicine genus *Dacetinops* Brown and Wilson was discovered only ten years ago. The original series included twelve workers and three dealate females collected by Edward O. Wilson in rain forest at the lower Busu River, near Lae, N. E. New Guinea. These specimens were described as *D. cibdella* by W. L. Brown and E. O. Wilson (1957), and a larva collected with them was characterized by G. C. and J. Wheeler (1957).

A second species, described below, has recently come to hand among material collected in Sarawak by Professor A. E. and Mrs. Eleanor Emerson. This significant and unexpected record robs *Dacetinops* of its apparent status as a New Guinean endemic. In the light of this discovery it would not be surprising if the genus was found to be more widespread in the Indo-Australian area.

DACETINOPS CONCINNA new species

Type locality. SARAWAK: Kapit District, Third Division, Nanga Tekalit Camp, 1° 38′ N, 113° 35′ E, January 29, 1963, A. E. and E. Emerson.

The holotype and paratypes were taken together in a dead log on the floor of virgin upland rain forest at an elevation of about 180 meters. Nanga Tekalit was a remote field camp established by the Chicago Natural History Museum, situated about 70 miles above Kapit on the Batang Balleh—Sungei Mengiong River system in western Sarawak.

[1] Research supported by U. S. National Science Foundation Grant No. GB 1634.

Type deposition. Holotype, two paratypes, and fragments of a third, all workers, deposited in the Museum of Comparative Zoology (type No. 31171).

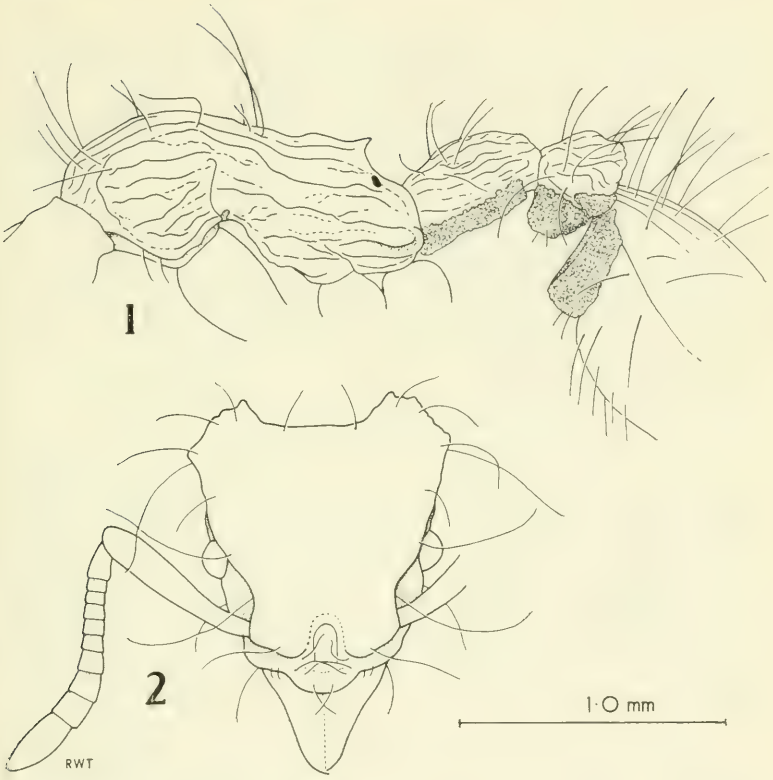
Description. The 3 intact type specimens have the following dimensions (holotype cited first). The parameters of measurement and the abbreviations are those of Brown (1953); measurements are given in millimeters: TL 4.8, 4.5, 5.0; HL 1.15, 1.12, 1.22; HW 1.02, 1.01, 1.09; CI 88, 90, 89; ML 0.35, 0.34, 0.38; MI 32, 30, 31; WL 1.47, 1.42, 1.57; petiole L 0.49, 0.45, 0.52; index of cephalic depression 59, 60, 59.

Form of head and mandibles as shown in Figure 2. Mandibles longer and more slender than in *D. cibdella;* outer borders distinctly concave; inner borders with about 15 very small, obtuse, backwardly directed teeth; apical tooth largest, more acute than remainder, which increase slightly in size towards the base. Antennal funiculus slightly incrassate, lacking a segmentally differentiated club. Palpal formula: maxillary 2, labial 2, structural details of palopmeres as in *cibdella* (Brown and Wilson, 1957, fig. 2). Antennal scrobes as in *cibdella;* longitudinal dividing carinae feeble; upper scrobe margins more broadly lamellate, almost completely obscuring posterior parts of scrobes in frontal view. Eyes proportionately larger and more convex, maximum diameter in holotype about 0.17 mm. Occipital lobes well developed.

Mesosomal profile (Figure 1) indented at metanotal area. Pronotal dorsum not margined anteriorly, submarginate at the sides. Propodeal structure and dentition as in *cibdella*, bases of teeth separated by slightly less than twice their length. Propodeal spiracles directed posterolaterally, placed well back on sides of propodeum, not as far back as in *cibdella*. Petiolar node longer than in *cibdella*, its dorsal profile more broadly and evenly arched. Postpetiole less transverse, subcircular in dorsal view. Gastric structure generally as in *cibdella;* first segment relatively narrow, elliptical in dorsal view, about 0.8 X as broad as long.

Yellowish white spongiform material developed on petiole, postpetiole and gaster, its distribution as in *cibdella*, the festoons less massive; tergal postpetiolar blocks separated from sternal mass on each side.

General sculpture consisting of very coarse longitudinal costulation, with a tendency towards reticulation due to the costular crests being slightly irregular in outline, and to the development of weak transverse ribs in the inter-costal grooves. Reticulation more distinct on posterior part of frons, occipital lobes, and especially



Dacetinops concinna sp. n., holotype worker. Fig. 1, mesosoma, petiole and postpetiole in lateral view. Fig. 2, head in frontal view; sculpturation omitted, and only hairs nearest the periphery shown.

on front of pronotum and postgenal areas of cranium; these parts also with a finely shagreened microsculpture superimposed on the costulae, which are generally smooth and shining elsewhere. About 10 costulae cross the cranium at its broadest point. Costae of mesosomal dorsum less cleanly cut than in *cibdella;* 4 distinct median ones along pronotal dorsum, with weak traces of another at the edge on each side. Sides of mesosoma coarsely and somewhat irregularly rugose.

Propodeal declivity smooth and shining, with several weak transverse carinae. Petiole and postpetiole moderately coarsely rugo-reticulate. First gastric segment moderately shining, with fine reticulate microsculpture; its basal half with about 10 sharp

straight longitudinal costae, the median four or five strongest, those at extreme sides almost vestigial and more closely spaced.

Mandibles smooth and shining. Antennae very finely shagreened. Antennal scrobes and coxae coarsely shagreened. Remaining leg segments finely shagreened, and with fine irregular longitudinal striae.

Long whitish body hairs extensively developed, proportionately longer than in *cibdella* (0.12–0.65 mm) but similarly distributed; many on head (particularly its margins), mesosoma and nodes occupying positions homologous to those of *cibdella*. Shorter erect to suberect hairs on legs and gaster, finer subadpressed ones forming a pilosity on underside of head, anterior faces of fore-coxae and tip of gaster.

Color almost exactly as in *cibdella*, deep reddish brown, mandibles, antennae, and legs dark yellowish brown.

Discussion. *D. concinna* is readily distinguished from *D. cibdella* by numerous characters, most of which are apparent on comparison of the published descriptions and figures of the two species. Nonetheless these ants constitute a compact and clearly delimited genus, and the generic diagnosis of Brown and Wilson requires only slight modification at this point. The statements concerning the antennal club structure, the mesosomal profile, and the mandibular shape and sculpturation need qualification, but these are minor matters.

REFERENCES

Brown, W. L., Jr.

1953. Revisionary studies in the ant tribe Dacetini. Amer. Midland Natur., **50** (1): 1–137 (pp. 7–15).

Brown, W. L., Jr., and E. O. Wilson

1957. *Dacetinops*, a new ant genus from New Guinea. Breviora, No. 77: 1–7.

Wheeler, G. C., and J. Wheeler

1957. The larva of the ant genus *Dacetinops* Brown and Wilson. Breviora, No. 78: 1–4.

(Received 15 September, 1965)

BREVIORA

Museum of Comparative Zoology

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AN EVALUATION OF JAMAICAN *DROMICUS* (SERPENTES, COLUBRIDAE) WITH THE DESCRIPTION OF A NEW SPECIES

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Grant (1938) evaluated the populations of *Dromicus* on the island of Jamaica and distinguished two species, *D. callilaemus* (Gosse, 1851), and *D. funereus* (Cope, 1862). His review was based upon the examination of only seventeen individuals, several of which lacked adequate locality data. The original descriptions incorporated data from only two specimens of *D. callilaemus* and three specimens of *D. funereus*.

Recently, much more material has been made available for study. A long series of *Dromicus* collected by Schwartz and others during the summer of 1961 together with material borrowed from several museums (a total of 227 specimens) has been utilized in the present study. The examination of a large number of individuals has made possible an analysis of the populations as well as an accumulation of data heretofore not present in the literature. A re-evaluation of the classification is necessary. The population regarded by Grant (1938) as *D. funereus* actually consists of at least two forms. Present evidence indicates that these forms are best treated as distinct species.

All measurements are in millimeters. The methods used in obtaining scale counts have been taken from Dowling (1951), and the terminology in regard to hemipenial descriptions has been derived mainly from Dowling and Savage (1960). Several paratypes of the new species have been deposited in the American Museum of Natural History (AMNH), and the University of Illinois Museum of Natural History (UIMNH), as well as in other collections.

Dromicus callilaemus (Gosse, 1851)

Natrix callilaema Gosse, 1851, Naturalist's Sojourn in Jamaica, p. 384. Type locality: Bluefields, Jamaica.

Since only two of the three (*fide* Boulenger, 1894:143) syntypes of *D. callilaemus* were examined for the present study, it seems expedient to designate one of these specimens as a lectotype, thus eliminating the possibility of confusion should the third specimen prove to be representative of a form other than *D. callilaemus.*

Description of the lectotype: British Museum (Natural History) 1946.1.5.90, Bluefields, Westmoreland Parish, Jamaica; juvenile, total length 157; tail length 57; ventrals 136; paired subcaudals 112; supralabials 7/7; infralabials 9/9; prefrontals 2; loreals 1/1; preoculars 1/1; postoculars 2/2; temporals 1 + 2/1 + 2; dorsals smooth, dorsal row formula 19-19-17. Internasal as long as broad, internasal suture considerably shorter than prefrontal suture; frontal longer than broad, much broader than supraoculars, about as long as its distance to the tip of the snout. A dark cap on the frontal scale, accentuated by darker pigmentation on the anterior portions of the supraoculars and the posteromedial borders of the prefrontals; cap narrowing posteriorly along the parietal sutures, diffusing into darker coloration on the neck; dorsum pale except for darker pigmentation in the area of the head and neck, pattern consisting of two rows of dark paramedian punctations on a light ground color and a dark lateral stripe incorporating scale rows 3, 4, and 5; venter pale except for dark mottling in the area of the chin and throat; dark pigmentation more concentrated along the sutures of the infralabials, supralabials and the anterior chin shields. Because of its small size the specimen could not be sexed; the subcaudal count, however, correlates with those of males from other localities.

Distribution: Jamaica, apparently island-wide.

Redefinition of species: A relatively small, slender, brick red snake with a distinct head pattern; ventrals 133-141 in males, 130-140 in females; anal divided; subcaudals paired, 106-122 in males, 92-109 in females; ventrals + subcaudals 242-262 in males and 231-242 in females; largest male 445, largest female 465; ratio of tail length to snout-vent length 0.57-0.75 in males and 0.50-0.73 in females; dorsal pattern usually consisting of three indistinct stripes, the lateralmost found on scale rows

3, 4 and 5, occasionally restricted to 3 and 4 or 4 and 5; pigmentation of stripes darker than ground color; venter pale, unmarked except for dark stippling or mottling in area of chin and throat, anterior scales often with light centers (Fig. 2, *left*); labials pale but mottled, flecked or stippled with darker pigmentation; a narrow dark bar extending from naris to the anterior border of the eye, bar continuing as a broad postocular stripe (Fig. 1, *top*); a dark cap on the frontal scale variously dilated to include portions of the supraoculars, prefrontals and

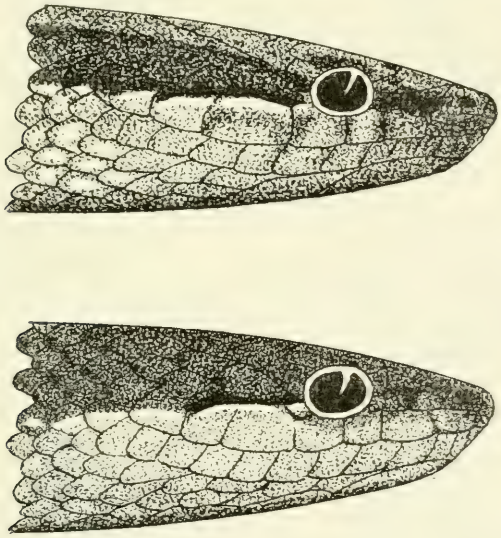

Fig. 1. *Top: Dromicus callilaemus*, lateral view of head, MCZ 69070, from Mona, St. Andrew Parish, Jamaica. *Bottom: Dromicus funereus*, lateral view of head, ASFS 15922, from Christiana, Manchester Parish, Jamaica.

nasals; cap usually narrowing posteriorly along the parietal sutures and continuing as a middorsal stripe, at times diffusing into the darker ground color of the neck; prefrontals, nasals, and supraoculars often with a dark spot; rostral pale, usually with a dark inverted U-shaped bar; pattern more pronounced in juveniles; young specimens also with many flecks or punctations on a lighter dorsum; supralabials 7/7; infralabials 9/9; prefrontals 2; loreals usually present 1/1; preoculars 1/1; postoculars 2/2; temporals 1 + 2/1 + 2; dorsals smooth, dorsal row formula 19-19-17.

Hemipenis (based upon the incompletely everted left organ of MCZ 69078) as follows: organ slightly bilobed, extending to the level of the ninth or tenth subcaudal; sulcus spermaticus bifurcating at the level of the third subcaudal; large spines near basal and midportions of the organ, remainder of organ covered with small spines.

The faded condition of the specimens examined precludes a detailed color description. The following comments have been appended from Barbour (1910): "All the Kingston specimens are red when adult with scattered marks on the sides of the head and throat. The young have a blackish stripe along the body and are spotted with dark brown. The throat and head are heavily marked with brown. The ground color, however, is the same as in the full-grown examples, viz., brick red."

Variation: Two specimens (USNM 108531 and MCZ 73761) have 8/9 and 5/8 infralabials, respectively; MCZ 7374 lacks both loreal scales, and MCZ 69073 maintains only the right loreal, considerably reduced in size; USNM 102650 has a dorsal row formula 19-17-17; temporal scale counts are generally 1 + 2/1 + 2, but these scales may be variously fused or divided.

Minor variation in color and pattern intensity is frequent. The head and dorsal pattern may be reduced, nearly absent, or somewhat obscured by darker pigmentation. This condition

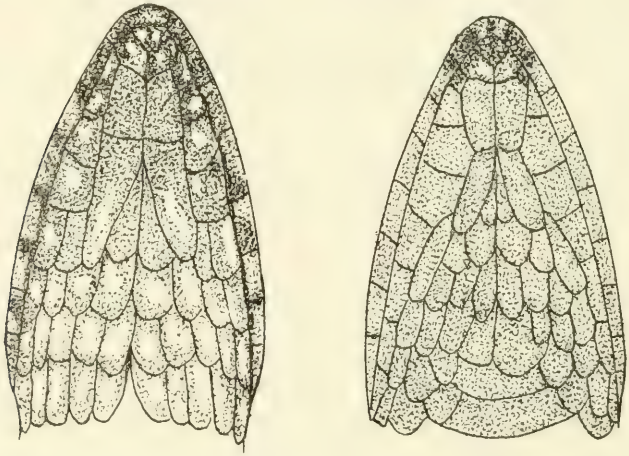

Fig. 2. *Left: Dromicus callilaemus,* ventral view of head, MCZ 52255, from Galloway Gap, St. Andrew Parish, Jamaica. *Right: Dromicus funereus,* ventral view of head, ASFS 15922, from Christiana, Manchester Parish, Jamaica.

occurs in several specimens from Montego Bay, Kingston, and Port Antonio.

Specimens examined: Jamaica, Westmoreland Parish, Bluefields, two (BMNH 1946.1.5.90 [lectotype], 1946.1.5.91 [paralectotype]); *St. James Parish,* Montego Bay, two (MCZ 52254, USNM 42881), Greenwood, one (SMIJ); *St. Elizabeth Parish,* Malvern, one (SMIJ); *Manchester Parish,* Mandeville, one (UMMZ 85948); *St. Andrew Parish,* Kingston and immediate vicinity, 47 (CM 33100, 33112; MCZ 7374, 18387, 44207-15, 44903-04, 52255, 53147, 66893, 69072-81, 69181, 73761; USNM 36662-63, 108079-80, 102650, 38947-48; UMMZ 85949, 85951; SMIJ [8 specimens]); *St. Thomas Parish,* Arntully, two (USNM 79637-38); *Portland Parish,* Boston Bay, two (USNM 108530-31), Windsor, one (USNM 117675).

Dromicus funereus (Cope, 1862)

Alsophis funereus Cope, 1862, Proc. Acad. Nat. Sci. Philadelphia, p. 77. Type locality: "Jamaica."

In view of the fact that the only specimen of *D. funereus* cited by number, by Cope, has been lost, as indicated by Stejneger in Grant (1938:85), the designation of a lectotype from the two extant syntypes is in order.

Description of the lectotype: USNM 12372, adult male; total length 378; tail length 140; ventrals 134; anal divided; paired subcaudals 90; supralabials 7/7; infralabials 9/9; prefrontals 2; loreal 1/1; preoculars 1/1; postoculars 2/2; temporals 1 + 2/1 + 2; dorsals smooth, dorsal row formula 19-19-17; internasals as long as broad; internasal suture slightly shorter than prefrontal suture; frontal slightly longer than broad, about twice as broad as supraoculars, about as long as its distance from the tip of the snout; loreal small, somewhat square; pigmentation dark, specimen appears somewhat faded; no discernible pattern.

Distribution: Western Jamaica, eastward as far as Bog Walk and Port Maria.

Definition: A relatively small, stout, brownish black snake, generally lacking a conspicuous head or dorsal pattern; ventrals 123-139 in males and 128-140 in females; anal divided; subcaudals paired, 78-91 in males, 62-78 in females; ventrals + subcaudals 203-224 in males and 192-218 in females; largest male 479, largest female 462; ratio of tail length to snout-vent length 0.43-0.59 in males, and 0.38-0.47 in females; tail length/snout-vent length ratio somewhat lower in juveniles than in adults;

dorsum generally dark, unpatterned; venter usually dark, similar in intensity to the dorsum, paler anteriorly in area of chin and throat with a suffusion of darker pigmentation (Figs. 2 and 4); juveniles often exhibiting a dorsal pattern of longitudinal stripes; head with a dark cap generally darker than the surrounding ground color, and venter darker than ground color of dorsum; supralabials 7/7; infralabials 9/9; prefrontals 2; loreals 1/1; preoculars 1/1; postoculars 2/2; temporals 1 + 2/1 + 2; dorsals smooth, dorsal row formula 19-19-17.

An account of the hemipenial configuration based upon the examination of the right extruded organ of ASFS 15172 is as follows: a single relatively slender, clavate organ extending to the level of the eighth subcaudal; sulcus spermaticus bifurcating on the apical surface with each branch terminating on opposite sides of a fleshy rowel (Fig. 3, *left*); organ virtually nude from the base to the level of the seventh subcaudal, thence becoming spinose to the apex, the spines generally small though somewhat larger on the non-sulcate surface.

Variation: Anomalies in numbers of certain head scales were occasionally encountered; scales involved were: supralabials,

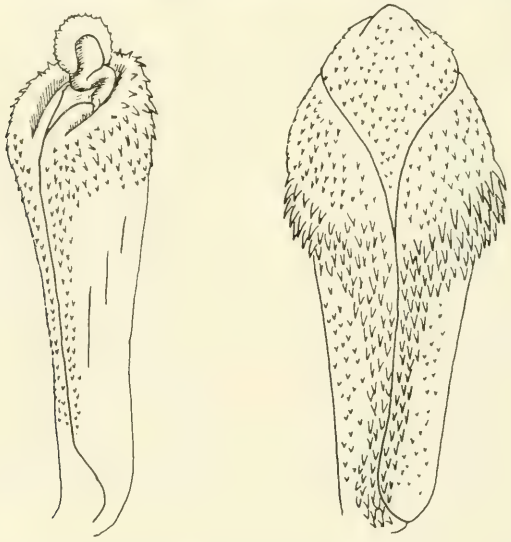

Fig. 3. *Left: Dromicus funereus,* hemipenis, view of sulcate surface, ASFS 15172, from 1 mi. S Reading, St. James, Jamaica. *Right: Dromicus polylepis,* hemipenis, view of sulcate surface, ASFS 13536, from Port Antonio, Portland Parish, Jamaica.

infralabials, prefrontals, preoculars and postoculars. Color variations appear negligible. ASFS 15991 and 15994 were noted as being partially erythrystic in life. Juveniles differ considerably from adults in possessing a relatively well marked dorsal pattern on a light ground color.

Specimens examined: Jamaica, St. James Parish, Montego Bay, two (USNM 108337-38), 5 mi. W Montego Bay, seven (MCZ 44897-900; UMMZ 85941-43), 1 mi. S Reading, 59 (ASFS 14743, 14932, 15060-63, 15066-67, 15146-48, 15159-77, 15264-92); *St. Elizabeth Parish,* Balaclava, two (USNM 73276-77); *Trelawny Parish,* Quick Step, one (USNM 117676), Windsor, two (USNM 83719-20); *Manchester Parish,* Christiana, 39 (ASFS 15827-29, 15916-25, 15982-16007), Mandeville, 12 (MCZ 13294-96, 44895-96, + two untagged specimens); USNM 31096, 108240-41; UMMZ 85946-47); Williamsfield, one (USNM 108533); *Clarendon Parish,* Grantham, eight (ASFS 16091-98); *St. Ann. Parish,* at mouth of Roaring River, one (MCZ 28092); *St. Mary Parish,* 4 mi. S Port Maria, two (MCZ 44901-02); *St. Catherine Parish,* Bog Walk, two (UMMZ 85944-45); *Jamaica* (no other locality designation) one (USNM 5780, paratype).

Dromicus polylepis new species

Holotype: MCZ 81020, an adult male, from Port Antonio, Portland Parish, Jamaica, collected 19 June 1961 by native Jamaican collector. Original number ASFS 13122.

Paratypes: Portland Parish, Jamaica, all from Port Antonio, as follows: AMNH 94171-75, native collector, 22 June 1961; AMNH 94176, USNM 152589, native collector, 23 June 1961; USNM 152590-92, native collector, 26 June 1961; UIMNH 56911-14, native collector, 27 June 1961; ASFS 13533-36, native collector, 28 June 1961; ASFS 13606-09, native collector, 30 June 1961; MCZ 81021, native collector, 29 June 1961; MCZ 7363-64 plus two untagged specimens (field tags 39 and 66), A. E. Wright, no date.

Associated specimens: Portland Parish, Port Antonio, one (field tagged specimen, number 65, duplicate of series MCZ 7363-64); *St. Andrew Parish,* Constant Spring, one (SMIJ), Cross Roads, one (SMIJ).

Distribution: Eastern Jamaica: known only from Portland Parish, Port Antonio, and St. Andrew Parish, Constant Spring and Cross Roads.

Diagnosis: A relatively small (largest male 455 mm, largest female 412 mm), slender (juveniles) to stout (adults), brownish black snake, usually lacking any conspicuous pattern; ventrals + subcaudals 230-245 in males, and 222-237 in females; hemipenis single, somewhat bulbous, and heavily spinose.

Description of holotype: An adult male, total length 387, tail length 150; ventrals 137; anal divided; paired subcaudals 106; head scalation typical of a generalized colubrid; internasals as long as broad, internasal suture slightly shorter than prefrontal suture; frontal longer than broad, broader than supraoculars, as long as its distance to the tip of the snout; loreal nearly square; supralabials 7/7; infralabials 9/9; prefrontals 2; loreals 1/1; preoculars 1/1; postoculars 2/2; temporals 1 + 2/1 + 2; dorsals smooth, dorsal row formula 19-17-17; dorsum dark brown to black with a pair of light brown lines of blotches, lower two or three scale rows paler; venter black, suffused with brown anteriorly.

Variation: Ventrals 136-141 in males, and 137-146 in females; paired subcaudals 92-106 in males, 76-93 in females; ventrals + subcaudals 230-245 in males, 222-237 in females; ratio of tail length to snout-vent length 0.44-0.63 in males, and 0.42-0.54 in females; supralabials 7/7; infralabials 9/9; prefrontals 2; temporals 1 + 2/1 + 2; a dorsal row formula of 19-19-17, occasionally 19-17-17; slight deviation from the normal number of head scales usually involving supralabials, infralabials, and postoculars.

An account of the hemipenial configuration based upon the examination of the right everted organ of ASFS 13536 (Fig. 3, *right*) is as follows: organ single, relatively stout and somewhat bulbous; apex extending to the level of the eighth or ninth subcaudals; sulcus spermaticus bifurcating at a distance from the base approximately equivalent to three-fifths the total length of the organ, each branch terminating in a fleshy apical papilla; a series of relatively large spines extending along either side of the unbranched portion of the sulcus, diverging laterally just proximal to the bifurcation of the sulcus and becoming confluent on the non-sulcate surface, forming four or five distinct rows at the level of the sixth and seventh subcaudals; spines somewhat reduced in size and number near the base of the organ; remainder of organ covered with small undifferentiated spines; a depression lateral to each apical papilla forming a fleshy ridge connecting the non-sulcate and sulcate surfaces.

Dorsum generally dark, unpatterned; venter usually dark, similar in intensity to the dorsum, paler anteriorly in area of

chin and throat with a suffusion of darker pigmentation; variations in color intensity negligible, young specimens tending to be somewhat lighter.

Comparisons: Although quite similar to *funereus* in coloration, *polylepis* may be distinguished on the basis of the total number of underbody scales and the configuration of the hemipenis. The ventral plus subcaudal counts of *polylepis* (230-245 in males, 222-237 in females) are more than those of *funereus* (203-224 in males, 192-218 in females) in specimens of the same sex, and the hemipenis is stout, bulbous, and heavily spined as opposed to the relatively slender, clavate, lightly spined and rowelled organ of *funereus*. In addition, males of *polylepis* have a higher subcaudal count (92-106) than males of *funereus* (78-91). There is no indication of overlap in distribution between the populations of these two species. Occurring sympatrically with *callilaemus* in eastern Jamaica, *polylepis* may be distinguished from the latter by its dark coloration and lack of conspicuous head and dorsal patterns. In addition to differences in the structure of the hemipenis, specimens of *polylepis* generally exhibit a lower subcaudal count (males 92-106, females 76-93) than specimens of *callilaemus* (males 106-122, females 92-109). The single-structured hemipenis of *polylepis* distinguishes it from the remaining forms of West Indian *Dromicus*, all of which are characterized by a bilobed organ.

Remarks: D. polylepis is the third species of *Dromicus* described from Jamaica. Except for this instance, not more than one species of *Dromicus* occurs on any one island in the West Indies. In general morphology, coloration, and pattern, *polylepis* is strikingly similar to *funereus,* and the two may be regarded as sibling species. In addition to *D. polylepis*, a lizard (*Anolis grahami aquarum* Underwood and Williams, 1959), and a hummingbird (*Trochilus polytmus scitulus* Brewster and Bangs; cf. Bond, 1956) have undergone differentiation in extreme eastern Jamaica, although in neither of these cases has the differentiation reached the status of species.

ACKNOWLEDGEMENTS

I wish to express my thanks to Dr. Albert Schwartz for use of specimens in the Albert Schwartz Field Series (ASFS), for obtaining the loan of the remainder of the specimens examined, and especially for his assistance in the laboratory; to Richard Thomas for his assistance in the laboratory as well as for the

illustrations of the hemipenes of *funereus* and *polylepis;* and to Ronald F. Klinikowski for the illustrations of the lateral and ventral head views of *callilaemus* and *funereus.*

For the loan of comparative material I wish to extend thanks to the following: James C. Bohlke and Edmond V. Malnate, Academy of Natural Sciences of Philadelphia; Miss Alice G. C. Grandison, British Museum (Natural History) (BMNH); Neil D. Richmond, Carnegie Museum (CM); Ernest E. Williams, Museum of Comparative Zoology (MCZ); C. Bernard Lewis, Science Museum, Institute of Jamaica (SMIJ); Charles F. Walker and George R. Zug, Museum of Zoology, University of Michigan (UMMZ), and Doris M. Cochran and James A. Peters, United States National Museum (USNM).

LITERATURE CITED

Barbour, Thomas

1910. Notes on the herpetology of Jamaica. Bull. Mus. Comp. Zool., **52**(15):273-301.

Bond, James

1956. Checklist of birds of the West Indies. Acad. Nat. Sci. Philadelphia, ed. 4, ix + 214 pp.

Boulenger, G. E.

1894. Catalogue of the snakes in the British Museum (Natural History). London, vol. 2, xiii + 382 pp.

Dowling, Herndon G.

1951. A proposed standard system of counting ventrals in snakes. British Jour. Herpetology, **1**(5):97-99.

——, and Jay M. Savage

1960. A guide to the snake hemipenis: a survey of basic structure and systematic characteristics. Zoologica, **45**(2):17-28.

Grant, Chapman

1938. The Jamaican *Dromicus funereus* re-established. Copeia, 1938:83-86.

Underwood, Garth, and Ernest Williams

1959. The anoline lizards of Jamaica. Bull. Inst. Jamaica, No. 9:1-48.

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B R E V I O R A

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SOUTH AMERICAN ANOLES: *ANOLIS BIPORCATUS* AND *ANOLIS FRASERI* (SAURIA, IGUANIDAE) COMPARED

By ERNEST E. WILLIAMS

INTRODUCTION

Confusion of the two species *Anolis biporcatus* Wiegmann 1834 and *Anolis fraseri* Günther 1859 first occurred in the original description of *A. fraseri* by Günther. One of the syntypes of *Anolis fraseri* Günther 1859 from western Ecuador was in fact a specimen of *Anolis biporcatus* Wiegmann 1834, a species first described from Mexico. Very unfortunately, it was this syntype which was sent to Paris for examination and which Bocourt (1873, pl. 15, fig. 12) figured as *A. fraseri*. The confusion of these two species which began thus has continued till the present.

Boulenger (1885) did, indeed, correct Günther's error and remove the *biporcatus* specimen from the syntype series, placing it in "*copii*" (=*copei* Bocourt 1873, a synonym of *biporcatus*[1]). He was, however, apparently quite convinced that "*copii*" and *fraseri* were closely related; he placed them side by side in his catalogue and a collation of his two descriptions shows only minor differences. This belief in a close relationship continues to the present day: L. C. Stuart (1955) in discussing the affinities of Central American *biporcatus* has suggested that *fraseri* is the South American representative of *biporcatus*.

A contrary view that *A. biporcatus* and *A. fraseri* are not at all close is also currently held. This opinion is implicit in Dunn's 1937 discussion of mainland giant anoles of the *latifrons* group. *A. fraseri* is placed with these, and *biporcatus* or its synonym *copei* goes quite unmentioned. Most recently a more explicit denial of close relationship has been propounded: R. Etheridge,

[1] See Stuart (1948) for discussion of the usage of the name *biporcatus* Wiegmann rather than *copei* Bocourt. The question is one of the identity of the Berlin type of *biporcatus*.

in a doctoral thesis (1960) at the University of Michigan, has placed *A. fraseri* and *A. biporcatus* in separate major sections of the genus *Anolis,* the first in his alpha series, the second in his beta series. (The primary distinction is the presence or absence of transverse processes on certain of the caudal vertebrae, an apparently trivial point which, however, has some very striking zoogeographic and other correlations.)

A. BIPORCATUS IN SOUTH AMERICA

Central to the confusion of *biporcatus* and *fraseri* has been the question of the presence of *biporcatus* itself in South America. This has been so poorly documented in the literature that doubt of the authenticity of the South American records has existed. Thus, while Burt and Burt (1933) list the range of *biporcatus* as "western Ecuador northward into Central America," Smith and Taylor (1950) give, instead, "Chiapas to Panama."

Boulenger, of course, had already listed one of the Günther syntypes from western Ecuador as the *biporcatus* synonym "*copii,*" but the absence of further records in the literature has probably progressively diminished for many workers the importance which has been attached to this single specimen. Thus, Barbour (1934), while mentioning the Günther syntype in the synonymy of *copei,* totally ignored it in his discussion of the range, which he regarded as extending only to Panama. Furthermore, the description from the Santa Marta Mountains of Colombia by Ruthven (1916) of *Anolis solifer,* regarded by him as a relative of *copei,* may have seemed to make the occurrence of *biporcatus* itself in South America still more improbable.

It is a measure of our ignorance of the *Anolis* of South America that confusion so extreme could exist regarding one of the larger and more distinct forms occurring there.

It is only because I have been able to see a quite unusual amount of material (some of it only recently collected) that it is possible to bring a measure of clarity into this muddled situation. I have been privileged to examine the material recently collected by James A. Peters (JAP) in Ecuador, as well as material in the American Museum of Natural History (AMNH), the Academy of Natural Sciences, Philadelphia (ANSP), the British Museum (BM), the Chicago Natural History Museum (CNHM), the Instituto La Salle, Bogota, Colombia (ILS), the Institut Royal des Sciences Naturelles, Brussels (IRSN), the Escuela Polytecnica, Quito, Ecuador (Orces), the Universidad Central de Venezuela (UCV), the University of

Michigan Museum of Zoology (UMMZ), the United States National Museum (USNM), the Vienna Museum (VM), and the Berlin Museum (ZMB). To the collectors and curators who have so generously loaned material I am deeply indebted. Dr. Fred Medem graciously donated Colombian material collected by him. National Science Foundation Grant GB 2444 supported this study.

On the basis of this newly examined material — so much more abundant than anything seen before — plus the collections of the Museum of Comparative Zoology, I have been able to come to the following conclusions.

1. *Anolis biporcatus* Wiegmann does occur in both Colombia and Ecuador and also in Venezuela.

2. *Anolis solifer* Ruthven must be considered a synonym of *A. biporcatus* Wiegmann.

3. *A. biporcatus* Wiegmann is at least in a broad sense sympatric with *A. fraseri* but the sympatric populations appear not to belong to the nominate race.

4. *A. biporcatus* belongs to a quite different group from *A. fraseri*, the relationships of which are, as Dunn and Etheridge have suggested, to endemic South American anoles.

COMPARISON OF *A. BIPORCATUS* AND *A. FRASERI*.

The characters of these two species — so often confused — are best compared in tabular fashion (Table 1). In many characters there is wide overlap. If in any numerical character the range

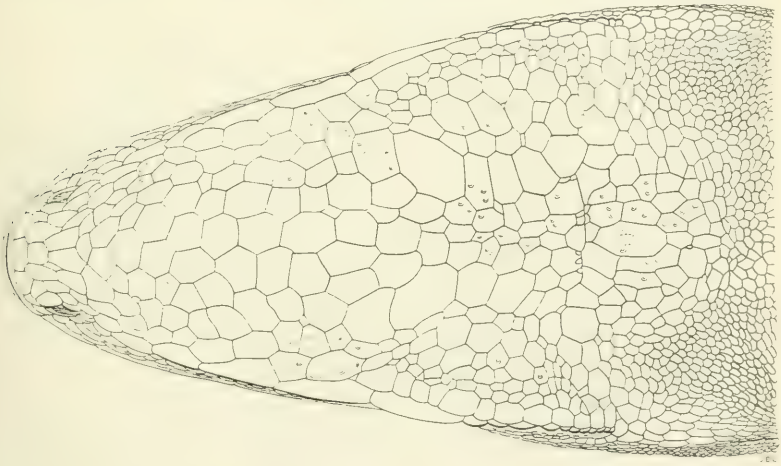

Fig. 1. *Anolis fraseri*, MCZ 70227. Dorsal view of head.

TABLE 1

South American biporcatus	*fraseri*
Head scales, at least anteriorly, keeled.	*Head scales never keeled, usually flat, pavementose, but sometimes swollen or wrinkled.*
2-3 scales between circumnasal and rostral.	1-2 scales between circumnasal and rostral.
Supraorbital semicircles separated by 0-3 scales.	*Supraorbital semicircles separated by 2-4 scales.*
Supraocular scales keeled.	*Supraocular scales smooth.*
2-3 more or less elongate supraciliary scales followed by a double series of scales which become smaller posteriorly and merge into granules like those medial to the series.	*Usually no elongate supraciliary scales; instead, the whole supraciliary margin of round or squarish scales distinctly larger than the granules medial to them.*
6-9 loreal rows.	4-9 loreal rows.
Interparietal small (but sometimes larger than the ear which is usually very small).	Interparietal larger (larger than the ear which is moderate in size).
Subocular scales usually completely and always at least partially separated from the supralabials by a row of intervening scales.	*Subocular scales broadly in contact with supralabials.*
7-12 supralabials to center of eye.	6-9 supralabials to center of eye.
Dewlap scales strongly keeled, almost as large as ventrals, rather uniformly distributed on the small fan.	*Dewlap scales smooth, small, almost granular, grouped in rows which are separated by naked skin.*
Ventral scales strongly keeled, mucronate.	*Ventral scales smooth or weakly keeled.*
22-26 lamellae under phalanges ii and iii of 4th toe.	20-24 lamellae under phalanges ii and iii of 4th toe.

in one species *completely* overlaps the known range of the other, I have omitted this character. The most striking differences are emphasized by italicizing the pertinent characters for *fraseri*. Both are large, short-legged, stout-bodied, relatively short-headed forms. The similarities are indeed amazing since the two species are, according to Etheridge, osteologically in totally different sections of the genus. The similarities would be even greater if Mexican and other northern *biporcatus* were compared with *fraseri* since the northern animals tend to have 3-4 scales between the supraorbital semicircles (*cf.* Stuart, 1955).

Overlapping variation in many features, as shown in Table 1, is characteristic of many sympatric species in *Anolis* and is one of the several reasons why this genus is described as "difficult." As in all such cases, the recognition of the valid species depends upon recognition of the constant (or almost constant) association of characters, however trivial. Smooth or keeled scales, suboculars in contact with or separated from supralabials, interparietal large or small are none of them characters universally useful in *Anolis*. The distinctive supraciliaries of *fraseri* are more useful because a substantial morphological gap between this condition and that shown by *biporcatus* will always distinguish these two species. (The *fraseri* supraciliaries occur, however, also and in a more exaggerated degree in *latifrons;* the condition is not unique to *fraseri*.)

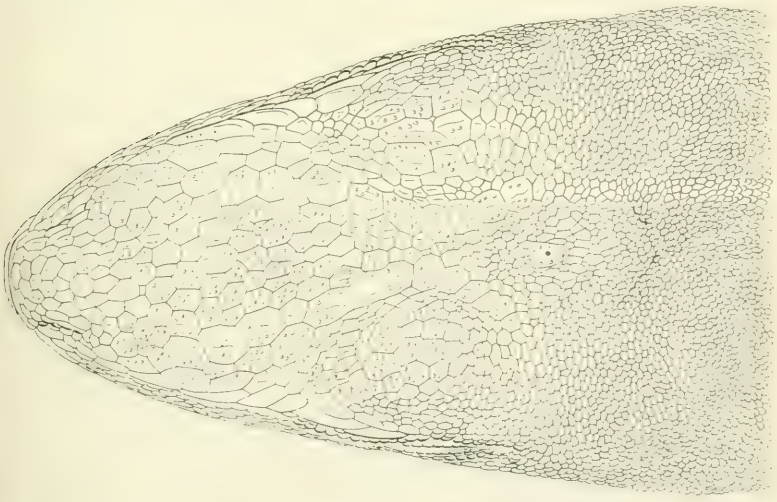

Fig. 2. *Anolis biporcatus parvauritus*, new subspecies, MCZ 78935. Dorsal view of head of type.

INTRASPECIES VARIATION: *A. BIPORCATUS*

While I have not endeavored to examine all specimens of *A. biporcatus* from all parts of its range, I have sampled the northern populations (Panama, Costa Rica, Guatemala, Mexico), and I have had the especial advantage of examining the series of 122 specimens taken by Slevin near Boquete, Panama (Slevin, 1942).[1]

Having seen this series I am impressed by the similarities of the various populations. There is indeed considerable variation within *A. biporcatus*, as I understand it. Thus, the number of scales between the semicircles, the number of scales between interparietal and semicircles, the number of loreal rows, the amount of keeling of the head scales, the contact or separation of suboculars and supralabials, and the length of the hind limbs all appear to be quite variable from individual to individual. Yet the species has a strong habitus character and is quite recognizable in spite of very striking variation.

A very few characters appear to sort out geographically. The supraocular scales and those surrounding the interparietal are extraordinarily small in Ecuadorian and southern Colombian specimens. In these same populations the ear opening is circular and very small in contrast to the rather oval opening of northern specimens.

Since there seem also to be some color differences of both body and dewlap in these same populations — which are precisely those sympatric with *fraseri* — it seems permissible to regard the Ecuadorian and southern Colombian animals as representing a distinct subspecies. Some discussion of available names is therefore required.

Anolis solifer Ruthven, type locality La Concepción, Santa Marta Mountains of northern Colombia, is the only name thus far proposed for a South American population of this species. That *solifer* does belong in *biporcatus* and may provisionally be synonymized with the nominate race seems clear from the comparison of the type with Panamanian and more northern material. The type of *solifer* can be matched by Panamanian material (except for the exceptionally short hind limbs) and Panamanian material is not separable by any constant characters from more northern specimens. The character of the very short hind limbs may define a population in northeast Colombia and Venezuela. One of the two available Venezuelan specimens has limbs as

[1] I am indebted to Dr. Allan Leviton of the California Academy of Sciences for this opportunity.

short as those of the *solifer* type but the other does not. In any event, the name *solifer* is clearly not available for the distinctive Ecuadorian and south Colombian populations. In the critical characters *solifer* resembles northern *biporcatus*.

The other names referable to the species *biporcatus* are equally unavailable. None of them refer to South American material. The nominate race *biporcatus* Wiegmann 1834 has the type locality "Mexico," now restricted to Piedra Parada, Chiapas. *A. copei* Bocourt 1873 has the type locality Santa Rosa de Pansas, Guatemala. *Anolis brevirostris* Peters 1873, next in date, has the type locality Chiriquí Prov., Panama. *Anolis brevipes* Boettger 1893 came from Cairo Plantation, La Junta near Limón, Costa Rica. Every one of these seems at present best grouped under the name *biporcatus*.

The southern race is thus without a name. In reference to the small ear it may be called:

Anolis biporcatus parvauritus new subspecies

Holotype: MCZ 78935, an adult ♂, "banana plantation, woods and penal colony camp, northern Gorgona Island, Cauca, Colombia, 5-45 meters altitude," collected by F. Medem and L. Salazar G., 1 to 23 February 1961.

Paratypes: **Colombia.** *Cauca:* MCZ 78933-34, 78936-41, same data as type. *Nariño:* MCZ 79142, Rio Mataje. **Ecuador.** *Esmeraldas:* USNM 157105, Cachavi; BM 1901.6.27.1, Carondolet;

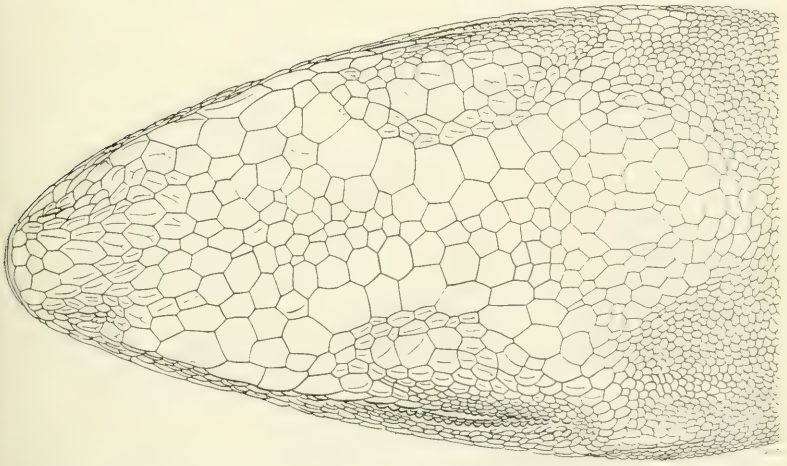

Fig. 3. *Anolis biporcatus biporcatus,* MCZ 56243, from Los Diamantes, Costa Rica. Dorsal view of head.

AMNH 6967, Rio Capayas; BM 1907.7.29.10-11, ZMB 18213, VM 12755, Rio Sapayo; BM 1901.8.3.1, Salidero; BM 1901.6.27.1, San Javier; Orces 3898, San Lorenzo. *Imbabura:* BM 98.4.28.13, Paramba. *Pichincha:* Orces 4596, Santo Domingo de los Colorados. "West Ecuador": BM 1946.8.13.21 (*fraseri* syntype). "Ecuador": USNM 20610, ANSP 7910.

Diagnosis. A subspecies of *Anolis biporcatus* distinguished by the small size of the scales surrounding the interparietal which are smaller than or only equal to middorsal scales (instead of distinctly larger than middorsal scales), by the small round ear rather ventrally placed (instead of a large oval ear extending well dorsally), and by a black-edged dewlap.

Comment. None of the conventional numerical counts in *Anolis* (e.g. scales across snout, scales between semicircles, scales between interparietal and semicircles, etc.) reveal the distinctness of *parvauritus,* though it is visually apparent immediately on inspection of the specimens (Figs. 2 and 3). The number of scales between interparietal and semicircles might be expected to correspond neatly to the very striking difference in the size of scales surrounding the interparietal in the nominate race and in *parvauritus.* In fact, however, there is wide overlap, and no discrimination could be based on the numerical character. However, comparison of the scales around the interparietal and the scales on the midline of midbody of the same animal gives instant conviction of the difference between the two races.

The character of the small size of supraocular scales is equally apparent on inspection. Here there is in *parvauritus* an absence of clear definition of any supraocular disk. This, however, is true also in many specimens of the nominate race. Here, again, comparison with middorsal scales (or direct confrontation with representatives of the northern race) convinces one of the existence of a difference. It is, however, a difference which is somewhat less striking than in the case of the scales surrounding the interparietal.

The size of the ear is again a character easily appreciated visually (Fig. 4), but it does not reveal itself by comparison with the size of the interparietal, which itself varies and may be very small. Comparison with the temporal area is more useful but the size and shape of the ear are sometimes distorted by preservation. Certain specimens seem intermediate: MCZ 79656-57 from Villa Arteaga, Antioquia, Colombia, have the ear round but rather large. In other regards (scales around interparietal, supraocular scales) these are northern in type. MCZ 79842 from Sincelejo,

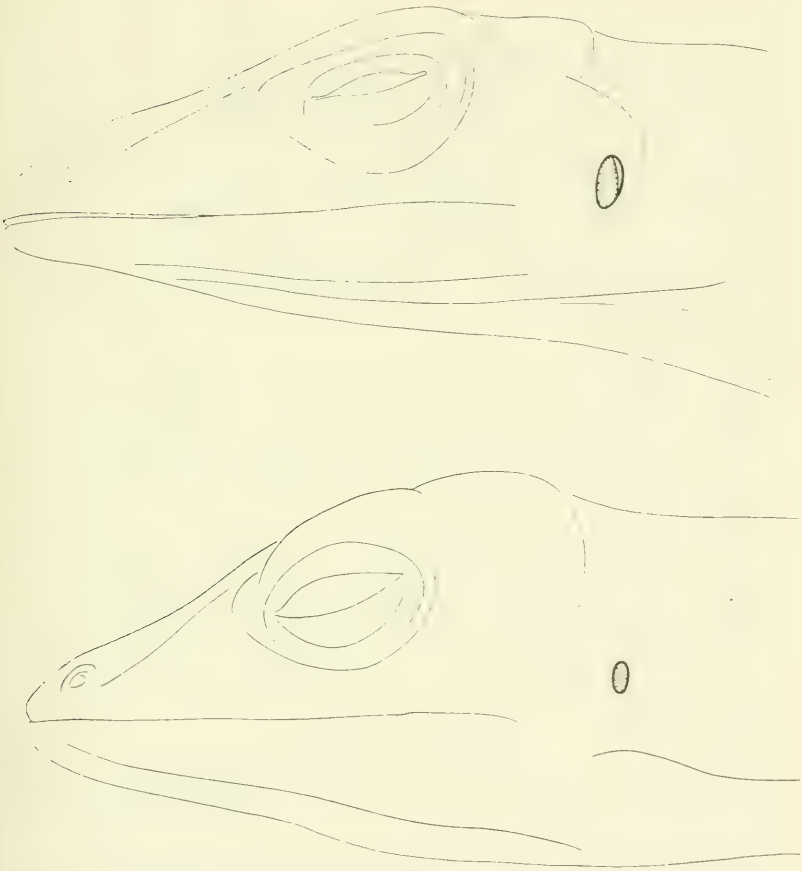

Fig. 4. Ear size in *A. biporcatus biporcatus* (top) and *A. biporcatus parvauritus* (bottom). Specimens are of the same snout-vent length.

Bolivar, on the other hand, has the ear small as in the southern race and the supraocular scales definitely large as in the northern race. A juvenile from Pizarro, Choco, Colombia (CNHM 43778), appears, in agreement with expectations from its geographic position, to be intermediate in size of ear and size of scales around interparietal and, like the nominate race, in size of supraocular scales. From this small sample one may perhaps infer that the ear character and the other characters that distinguish the races vary erratically and not in any correlated fashion in northern Colombia.

The color of the southern race seems different in preserved specimens from that of any northern animals including the northern Colombian intermediates, but this is very difficult to define in animals with strong powers of color change. In the Gorgona Island material, which is the largest series and the most recently collected, there is strong reticulation enclosing light areas which may, in animals in the dark phase, give an appearance of light spotting. This reticulation tends to extend to the belly, but the throat is not spotted with darker as it typically is in the northern race. The north Colombian intermediates also lack throat spotting but otherwise seem like other northern populations in color.

The small dewlap is conspicuously black in preserved specimens of the southern race. Examined under the microscope, it is seen that the scales are intensely black while the skin may have a trace of red. According to F. Medem's notes on the Gorgona Island series, the dewlap in life is orange and red at the center, black at the edge.

Slevin's 1942 notes on the nominate race at Boquete, Chiriquí, Panama, contrast with this: "The rather large dewlap of the males had a ground color of orange with rows of bluish scales."

Duellman (1963) has described the dewlap of a specimen from 20 km NNW Chimapa, Guatemala, in very similar terms, as having "the outer part pale orange, the median part purplish blue." J. M. Savage has sent me a diagram of dewlap coloration in a male from the Tilaran area in northwest Costa Rica. From this it appears that the free edge of the dewlap is red-orange while a small anterior part of the base is white, a larger posterior portion powder blue.[1]

These three descriptions, all in essential agreement, are from specimens which bracket much of the range of the typical race and indicate a dewlap color consistently and sharply different from that of the southern race. Unfortunately, the dewlap color in Venezuelan specimens, for which "*solifer*" is an available name, is unknown.

Behavioral notes. F. Medem (field notes) remarks on the Gorgona Island topotypic series of *parvauritus* that the gular sac is "extended *laterally*" and that this species is here found

[1] The description by Taylor (1956, p. 136) of the dewlap of Costa Rican specimens as "white or slightly greenish" appears on careful reading to result from a complex confusion of notes for *A. capito* with the text for *A. biporcatus*, and apparent resulting omission of some of the pertinent data for *biporcatus*. See the reference to *A. capito*, top of page 137.

on trees up to 5 meters or more in height, rarely on the ground. It is seen most often early in the morning (7:30-9:30 AM).

A. biporcatus is everywhere known as a strongly arboreal species. Slevin (1942) reports on it at Boquete, Panama, as follows: "It was generally found in the larger and higher trees, but occasionally on fence posts and once or twice on the ground. While most frequently seen on the tree trunks, it was often discovered on fairly high limbs, crouching down as if to avoid detection." This compares very well with Medem's notes on *parvauritus,* and the two races are probably very similar ecologically.

INTRASPECIES VARIATION: *A. FRASERI*

A. fraseri, with a much smaller geographic range and a smaller available sample, seems rather consistent in scale characters.[1] There is no hint of racial differentiation. In color, however, there are two striking variants: strong transverse banding extending onto flanks (see fig. 3 in Williams, 1963), or the restriction of alternate light and dark to the vertebral zone. This statement, of course, applies to preserved specimens; there is unfortunately no information on color in life and these two patterns may very well be part of the repertoire of one individual.

THE DISTRIBUTION OF THE TWO SPECIES IN SOUTH AMERICA

The number of specimens of *A. fraseri* and of South American *A. biporcatus* that I have been able to examine is large only by the standards peculiar to the generality of South American anoles: for *A. fraseri,* 14 specimens; for *A. biporcatus,* 32. *A. biporcatus,* as may often be true for an invader from Central America, extends not only down through the Chocoan area of Colombia into Ecuador west of the Andes but also along the northern edge of Colombia in the Santa Marta Mountains into Zulia and Táchira in Venezuela. *A. fraseri* — a South American endemic — is apparently restricted to Colombia and Ecuador west of the Andes, and is mainly Ecuadorian. I list below the

[1] *Anolis devillei* Boulenger 1880 (type examined) is an unequivocal synonym of *A. fraseri* Günther 1859, and Boulenger (1885) himself synonymized it. The juvenile specimen referred to *devillei* by Boulenger (1880) is very poorly preserved and indeterminable; Boulenger utilized it with great hesitation.

South American *A. biporcatus* examined (except for the paratypes of *parvauritus*, which have been listed previously) and also all specimens of *A. fraseri*.

Anolis biporcatus. **Colombia.** *Antioquia*. Villa Arteaga, MCZ 79656-57. *Magdalena*. La Concepción, Santa Marta Mtns., MCZ 6549 (type of *solifer* Ruthven). *Bolivar*. Sincelejo, MCZ 78942. Turbaco (?), Leiden 2807. *Norte de Santander*. Near Rio Zulia, 32 km N Cúcuta, ILS 19. *Choco*. Pizarro, CNHM 43778. **Venezuela.** *Táchira*. La Fría, UMMZ 55994. *Zulia*. La Kasmera, Parija 300 m, UCV 8023. ? **Brasil.** "Silva, See Saraca," VM 5904.[1]

Anolis fraseri. **Colombia.** *Cauca*. Buenaventura, CNHM 43771; El Tambo, ANSP 25563; Jamundí, CNHM 43772. **Ecuador.** *Esmeraldas*. San Mateo, CNHM 27681. *Imbabura*. Apuela, JAP 4331. *Pichincha*. Mindo, UMMZ 55525; Nanegal, BM 83.2.23.11, JAP 925; Quito, BM 72.2.26.16. *Guayas*. Rio Pescado, nr. Naranjal, AMNH 23432; Bucay, AMNH 23030. *El Oro*. 7 km SE Buenavista, JAP 2485. "West Ecuador": BM 60.6.16.36 (1946.8.8.47) (lectotype of *fraseri*). "Equateur": IRSN 2006 (type of *devillei* Boulenger).

REFERENCES CITED

Barbour, T.

1934. The anoles. II. The mainland species from Mexico southward. Bull. Mus. Comp. Zool., **77**: 121-155.

Boettger, O.

1893. Katalog der Reptilien-Sammlung im Museum der Senckenbergischen naturforschenden Gesellschaft in Frankfurt am Main. I Teil. (Rhyncophalen, Schildkröten, Krokodile, Eidechsen, Chamäleons). x + 140 pp. Frankfurt-a-M.

Bocourt, F.

1873. Études sur les reptiles. Mission scientifique au Mexique et dans l'Amerique Centrale. Pt. 3. Sauriens. Livr. 2: 33-112. Paris.

Boulenger, G. A.

1880. Reptiles et batraciens recueillis par M. Emile DeVille dans les Andes de l'Equateur. Bull. Soc. Zool. France, 1880: 41-48.

1885. Catalogue of the lizards in the British Museum (Natural History), **2**: ix + 497 pp. London.

Burt, C. E. and M. D. Burt

1931. South American lizards in the collection of the American Museum of Natural History. Bull. Amer. Mus. Nat. Hist., **61**: 227-395.

[1] I assume that this is Lago Saracá, Amazonas, but this locality is very remote from any other record. There are no other specimens of *biporcatus* from Brasil. Locality records in the Vienna Museum are so often erroneous that I cannot accept this without confirmation.

Duellman, W. E.
1963. Amphibians and reptiles of the rain forests of southern El Peten, Guatemala. Univ. Kansas Publ. Mus. Nat. Hist., **15**: 205-249.

Dunn, E. R.
1937. The giant mainland anoles. Proc. New England Zool. Club, **16**: 5-9.

Etheridge, R.
1960. The relationships of the anoles (Reptilia: Sauria: Iguanidae): an interpretation based on skeletal morphology. University Microfilms, Inc., Ann Arbor, Michigan.

Günther, A.
1859. Second list of cold-blooded vertebrates collected by Mr. Fraser in the Andes of western Ecuador. Proc. Zool. Soc. London, 1859: 402-420.

Peters, W.
1874. Über neue Saurier (*Spoeriodactylus, Anolis, Phrynosoma, Tropidolepisma, Lygosoma, Ophioscincus*) aus Centralamerica, Mexico, und Australien. Monatsber. Akad. Wiss. Berlin, 17 November 1873: 738-747.

Ruthven, A.
1916. Three new species of *Anolis* from the Santa Marta Mountains, Colombia. Occ. Pap. Mus. Zool. Univ. Michigan, **32**: 1-8.

Slevin, J. R.
1942. Notes on a collection of reptiles from Boquete, Panama, with the description of a new species of *Hydromorphus*. Proc. California Acad. Sci., Ser. 4, **23**: 463-480.

Smith, H. and E. H. Taylor
1950. An annotated checklist and key to the reptiles of Mexico, exclusive of the snakes. Bull. U. S. Nat. Mus., **199**: 1-253.

Stuart, L. C.
1948. The amphibians and reptiles of Alta Verapaz, Guatemala. Misc. Publ. Mus. Zool. Univ. Michigan, **69**: 1-109.
1955. A brief review of the Guatemalan lizards of the genus *Anolis*. Misc. Publ. Mus. Zool. Univ. Michigan, **91**: 1-31.

Taylor, E. H.
1956. A review of the lizards of Costa Rica. Univ. Kansas Sci. Bull., **38**: 1-322.

Wiegmann, A. F. A.
1834. Herpetologia Mexicana. Berlin, vi + 54 pp.

Williams, E. E.
1963. Studies on South American anoles. Description of *Anolis mirus*, new species, from Rio San Juan, Colombia, with comment on digital dilation and dewlap as generic and specific characters in the anoles. Bull. Mus. Comp. Zool., **129**: 463-480.

(Received 15 September 1965.)

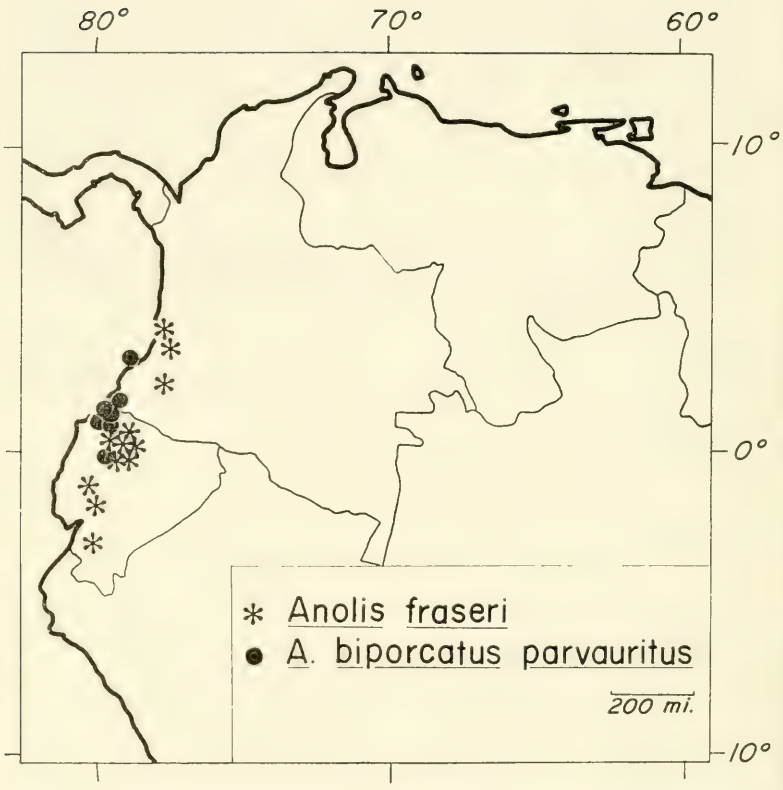

Fig. 5. Map of distributions of *A. fraseri* and *A. b. parvauritus*. Intermediates and representatives of the typical race of *biporcatus* in northern Colombia and Venezuela omitted.

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS. FEBRUARY 25, 1966 NUMBER 240

GYMNOTHORAX GALETAE, A NEW MORAY EEL FROM THE ATLANTIC COAST OF PANAMA

By

IRA RUBINOFF

Museum of Comparative Zoology, Harvard University

The collection of fishes which included this new species was taken by the author in 1962 at Galeta Island on the Atlantic Coast of Panama. The type locality is identical to that from which Rubinoff and Rubinoff (1962) reported several new Panamanian records of apodes.

The fish here described as new is immature and unique. It is nevertheless described because of the proposed construction of a sea-level canal across the Middle-American Isthmus. The removal of this land barrier to interoceanic dispersal places an obligation upon biologists for a thorough pre-canal recording of the populations and distributions of marine fishes in this still relatively poorly studied region.

Family MURAENIDAE

Genus GYMNOTHORAX Bloch 1795

GYMNOTHORAX GALETAE, new species

Figure 1

Type locality: Rubinoff Station No. 79, Galeta Island, 9°24′20″N 79°52′18″W Canal Zone, Atlantic Coast of Panama. Collected at a depth of less than 6 inches from the flat of reef, with "Pro-Noxfish" that was introduced to the seaward edge of the reef and which was rapidly dispersed over the reef by the flooding tide, 1300 hrs., 25 May 1962.

Measurements of the holotype (in mm): MCZ 44035, an immature fish. Total length 128, head and trunk 59.0, tail 69, head 16.5, snout 2.7, eye 1.7, depth at gill opening 6.1, depth at anus 5.1, cleft of mouth 6.6, length of gill opening 1.1, fleshy interorbital 2.0, snout to origin of dorsal fin 11.8, diameter of typical body spot 3.

Description: Body elongate, somewhat laterally compressed, this compression somewhat more pronounced posteriorly. Greatest body depth about 21 in total length. Head and trunk shorter than tail by about six-tenths of the length of the head. Head 7.75 in total length. Eye 9.7 in head, 1.6 in snout. Snout 6 in head. Cleft of mouth 2.5 in head, mouth closing completely, teeth all enclosed by lips. Fleshy interorbital 8.25 in head. Dorsal fin inserted well in advance of gill opening, distance from snout to dorsal insertion about 1.4 in head. Anal fin beginning immediately behind anus. Dorsal fin confluent with anal around tip of tail. No paired fins present. The anterior nostrils are simple tubes. The posterior nostrils have slightly raised rims and are above and slightly in advance of the margins of the eyes. There are two pores just anterior to and slightly above the gill slits. There are four pores along the margin of the upper jaw and five along the lower jaw. The total number of vertebrae, as determined by X-ray, is 158.

The terminology of the following description of the dentition corresponds to that of Ginsburg (1951). Upper "jaw teeth" include 4 anterior and 14 posterior teeth on the left side, with 9 anterior and 10 posterior teeth on the right side. The "premaxillary" has 3 enlarged canines, and there are 7 small conical "palatal teeth." The dentary has an outer row of 19 teeth on the left side, and 21 on the right. Anteriorly, 4 enlarged canines are present on each side medial to the outer dentary series.

Color description: The following color observations are made from Kodachrome II photographs which were taken immediately after the capture of the specimen. Head light orange-brown, without spots. Snout maroon, darker than rest of head (considerably darker than indicated in the Figure). Anteriormost spot above, and just posterior to origin of dorsal fin. Laterally, maroon-brown spots begin at the level of the gill slits and continue posteriorly with approximately equal density and size to the margin of the tail where the confluence of the dorsal and anal fin is pigmented light orange, a hue similar to that of the head. Between the pale orange of the head and tail, the background is a pale reddish brown. Thin striae of maroon pigment radiate from the dense circular lateral maroon spots. These lateral spots are generally quite discrete, with the margins of two adjacent spots only occasionally overlapping. The spots do not look as if they might merge to form a reticulated pattern with growth. Upon preservation the body spots have become brown and the orange color of the head and tip of the tail has changed to a pale reddish brown matching the rest of the body ground color, which has remained relatively unchanged.

Remarks: Gymnothorax galetae does not resemble the adult or immature stages of any other Atlantic species of *Gymnothorax*. It is readily distinguished from all other Atlantic species by its large maroon spots on a paler ground color. Immature specimens of *G. moringa* and *G. vicinus* are common inhabitants of reef interstices at Galeta Island. The possibility that the present species might be a color variant of these species has been considered but eliminated by a comparison of their total number of vertebrae: *ca.* 135 for *G. vicinus, ca.* 141 for *G. moringa,* and 158 in the type of *G. galetae.*

Due to the proximity of the type locality to the Panama Canal, Eastern Pacific members of the genus *Gymnothorax* were also examined for possible evidence of affinities to the new species. There are, however, no records of members of this genus entering brackish and fresh waters of the Panama Canal System (Hildebrand, 1938, and personal observation at draining of Gatun Locks in 1961). The color patterns of several Indo-Pacific species such as *G. isingteena* and *G. stellatus* superficially resemble the pattern of *G. galetae.* However, these can be readily distinguished by the continuation of their body spotting onto the head. The head of *G. galetae* is not spotted.

The relationships among the species of *Gymnothorax* are in general too poorly understood to further attempt to discuss the affinities of the new species, particularly in view of the limited material available.

ACKNOWLEDGMENTS

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LITERATURE CITED

Ginsburg, I.

1951. The eels of the northern Gulf Coast of the United States and some related species. Texas Journal of Science, **3** (3): 431-485.

Hildebrand, S. F.

1938. The Panama Canal as a passageway for fishes, with lists and remarks on the fishes and invertebrates observed. Zoologica (N. Y.), **24** (3): 15-45.

Rubinoff, I., and R. W. Rubinoff

1962. New records of fishes from the Atlantic Coast of Panama. Breviora, No. 169: 1-7.

(Received 20 September 1965.)

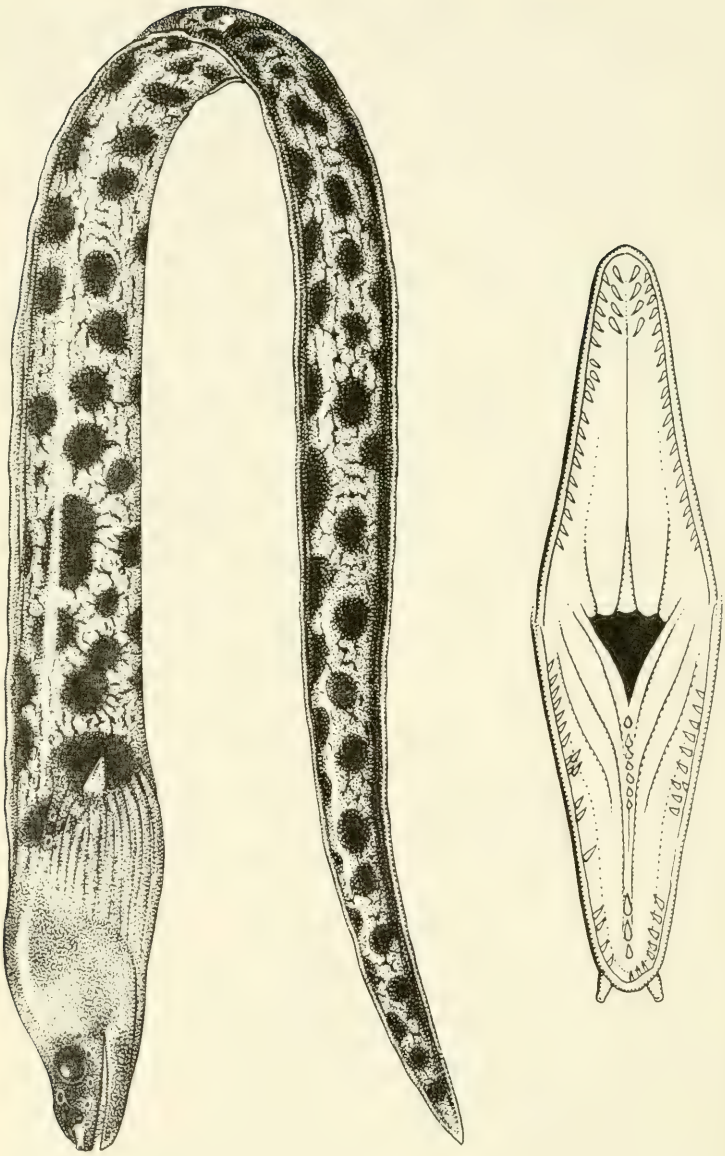

Figure 1. Lateral view, and open gape of *Gymnothorax galetae*. (Drawn by Nicholas Strekalovsky.)

BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. FEBRUARY 25, 1966 NUMBER 241

AVOCETTINOPS YANOI, A NEW NEMICHTHYID EEL FROM THE SOUTHERN INDIAN OCEAN

By GILES W. MEAD and IRA RUBINOFF

Museum of Comparative Zoology, Harvard University

The oceanic eels of the genus *Avocettinops* lack the prolonged jaws or snout typical of other snipe eels, although they do have fleshy anterior appendages; and they can be distinguished from all other apodal fishes by the complete absence of teeth, if not from their bizarre physiognomies alone. The number of known specimens is small: the type of *A. schmidti* (Roule and Bertin, 1924); a second specimen taken off Zanzibar during the "John Murray" expedition (Norman, 1939; the specimen rather casually christened *Avocettinops normani* by Bertin in 1947); a specimen collected from the *Arcturus* by William Beebe, New York Zoological Society, off New York and reported as *A. schmidti* by Böhlke and Cliff (1956) (SU 47758); and the fish described below. Böhlke and Cliff (1956) also discussed in some detail the nomenclatorial and taxonomic entanglements generated by earlier authors, and reviewed the relationship of the genus to other snipe eels.

AVOCETTINOPS YANOI, new species

Figure 1

Holotype. — A specimen 620 mm long collected by R/V *Anton Bruun* during the International Indian Ocean Expedition, Cruise VI, Sta. 350 B, APB label 7314; 27 June 1964; 28°05′ S, 64°58′ E to 28°28′ S, 65°04′ E; depth of bottom 2200-4000 m; 10-ft. Isaacs Kidd Midwater Trawl with catch dividing device nominally set to operate at 350 m; deep fraction of catch the probable depth of capture between the maximum depth reached, 1750 m and 125 m. MCZ Catalog No. 44404.

Distinctive characters. — *Avocettinops yanoi* differs from its congeners in the position of the dorsal fin, which originates well in advance of the gill slit, and by the more anterior anal origin, the preanal distance being about 1.3 times the length of the head (*cf.* 2.0 or 2.1 in specimens hitherto described). The species has a correspondingly low number of preanal vertebrae (13 *cf.* 20 or more), and of lateral line pores between the temporal pore and that above the origin of the anal fin (13 *cf.* 18 or more).

Description. — Meristic data and measurements, which are expressed in per cent of head length to facilitate comparison with prior catches, are provided in Table 1.

Body about two-thirds as broad as deep anteriorly, becoming more compressed posteriorly. Head 12 in total length. Jaws coterminal and bearing fleshy protuberances anteriorly both of which were damaged during capture. Angle of gape under posterior edge of eye. Mouth without teeth but with minute denticles on skin overlying jaws and roof of mouth. Anterior nostril before center of orbit, the tube anteriorly directed. Posterior nostrils large deep pits, the posterior edges of which lie on a tangent with anteriormost points of orbits. Gill slits short (13 in length of head), ventrally directed, and placed below bases of pectoral fins. Eye circular, its diameter 7 in length of head. Acustico-lateralis system on head well developed (Fig. 1), the pores large. The system includes series of lappets, which are presumably sensory, such as the vertical row behind and the horizontal series above and behind the eye. Similar lappets are interspersed at irregular intervals between pairs of pores in the lateral line along the flank. These lappets are not bilaterally symmetrical. The lateral line is continuous and complete.

Dorsal and anal fins originating far forward and nearly continuous around tip of tail. Predorsal distance 17 in total length, preanal 10 in length. Pectoral fin broad, short, and lying in a horizontal plane when expanded. Anus and urogenital openings immediately anterior to origin of anal fin. The fish is completely black externally. Internally, the peritoneum, linings of mouth, and pharyngeal cavities are white. The coelom extends posteriorly far beyond the anus to about the midpoint of the total length. Most of this space is filled by the swollen, convoluted and apparently mature pair of gonads. These appear to be ovaries, although they are too decomposed for close study. The muscular stomach, which is placed anterior to the anus, is empty.

The success of any trawling expedition is dependent in no small measure on those responsible for the maintenance and operation of the nets and associated equipment. Throughout the trawling activities which produced the collections of which this specimen is a part, Mr. Shigeru Yano and his associate, Mr. C. P. Lee, devoted themselves to this equipment with ability, understanding, and scrupulous care; without these master fishermen these cruises would have fallen short of their goals. With respect and professional admiration we take pleasure in naming this new eel in honor of Shigeru Yano, friend and fellow fisherman.

Remarks. — The identity of the nominal species of *Avocettinops* remains in doubt. The type of *A. schmidti* has been cleared in potassium hydroxide and stained with alizarine. Norman's "John Murray" specimen from off Zanzibar lacks the tail, and has a fragmentary head which has also been cleared and stained, while the Atlantic individual discussed by Böhlke and Cliff is also fragmentary. Hence meaningful morphological comparison is impossible. A qualitative study of the latter specimen and the published accounts of the two others, in comparison with *A. yanoi*, suggests that the Zanzibar specimen is probably identical with *A. schmidti*, while the western North Atlantic specimen of Böhlke and Cliff probably represents a distinct and unnamed species.

This specimen was taken during the American Program in Biology, International Indian Ocean Expedition, a program financed by the National Science Foundation and under the general scientific direction of Dr. John H. Ryther of the Woods Hole Oceanographic Institution. To the National Science Foundation, which has also financed the research of which this is a part through GF 147 with Harvard University, and to Dr. Ryther the authors express here their sincere appreciation.

TABLE 1

Proportional dimensions, expressed as per cent of length of head, of *Avocettinops schmidti* and *A. yanoi*. Data for the type of *A. schmidti* taken from the descriptions and figures of Roule and Bertin (1924, 1929); those of the Stanford University specimen from Böhlke and Cliff (1956), and from the specimen.

	Type of *A. schmidti*	Western North Atlantic (SU 47758)	Type of *A. yanoi*
Total length (mm)	510.0	—	620.0
Length of head (mm)	32.0	32.0	50.0
Depth of body at anus (% of h.)	21.9	—	24.4
Greatest depth of body	43.8	28.4	35.8
Width of body at anus	9.4	*ca.* 7.8	15.4
Greatest width of body	10.9	—	16.4
Greatest depth of head	25.6	*ca.* 23.4	26.4
Greatest width of head	18.8	17.5	19.8
Length of snout	25.0	25.0	24.0
Diameter of orbit	15.6	12.5?	13.4
Postorbital length of head	59.4	55.9	62.4
Length of upper jaw	39.1	33.1	34.8
Length of lower jaw	32.8	24.7	32.8
Length of gill slit	13.1	17.2	7.6
Interorbital width	14.1	—	16.6
Predorsal length	90.6	108.8	73.8
Preanal distance	203.1	207.8	127.4
Width of base of pectoral fin	14.1?	9.7	9.0
Length of pectoral fin	28.1	24.7	29.0
Dorsal fin rays	340	—	285
Anal fin rays	315	—	266
Pectoral fin rays	16-17	15-15	12-13
Total number of vertebrae	194	—	184
Preanal vertebrae (±1)	20	24	13
Total number pores in lateral line	188	—	185
Lateral-line pores, temporal pore to anus	18?	23	13

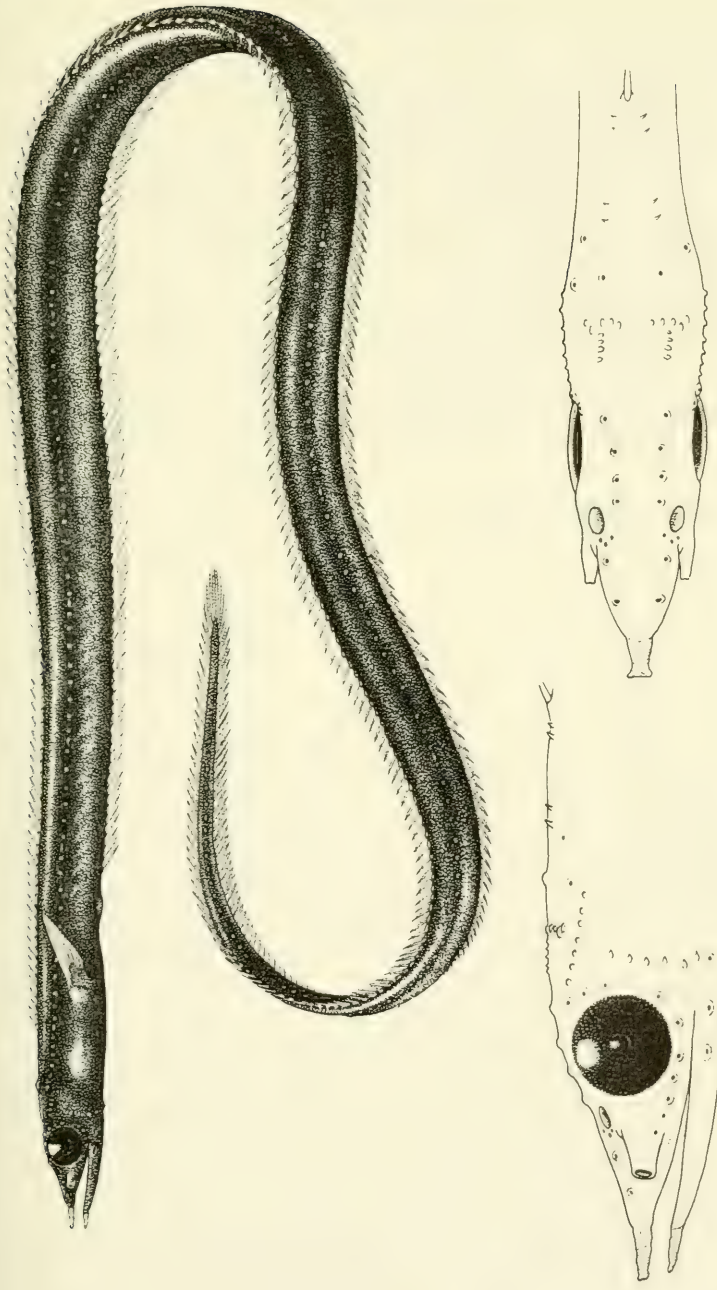

Figure 1. *Avocettinops yanoi*, holotype, 620 mm in total length, MCZ 44404. (Drawn by Nicholas Strekalovsky.)

LITERATURE CITED

Bertin, Léon

1947. Notules ichthyologiques. 1. — Compléments sur le genre *Avocettinops*. Bull. Soc. Zool. France, **72**:54-55.

Böhlke, James E., and Frank S. Cliff

1956. A discussion of the deep-sea eel genus *Avocettinops*, with notes on a newly discovered specimen. Copeia, 1956:95-99.

Norman, J. R.

1939. Fishes. Sci. Rep. "John Murray" Expedition, **7**(1):116 pp.

Roule, Louis, and Léon Bertin

1924. Notice préliminaire sur la collection des nemichthydés recueillie par l'expédition du "Dana," (1921-1922), suivie de considérations sur la classification de cette section des poissons apodes. Bull. Mus. Nat. Hist. Natur., Paris, **30**:61-67.

1929. Les poissons apodes appartenant au sous-ordre des Nemichthydiformes. Rep. "Dana" Exp., 1920-1922, No. 4, 113 pp., 19 pls.

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BREVIORA

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THE SUPPOSED "SPONGE SPICULES" OF MERRILL, 1895, FROM THE LOWER CRETACEOUS (ALBIAN) OF TEXAS

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INTRODUCTION

In 1895, a paper was published by J. A. Merrill giving the results of a study of chert nodules from Texas. In this he described and figured a number of microscopic structures which were interpreted as sponge spicules and referred, hesitantly, to six known genera; eight new species were proposed, all of which were doubtfully attributed to the living genus *Geodia*.

This work escaped attention until 1945, when Glaessner noted that the supposed spicules of *Geodia* were in fact hystrichospherids (p. 20). As such, they constitute the first Lower Cretaceous hystrichosphere assemblage and hence the first record of Mesozoic dinoflagellate cysts from the United States. Subsequently, the present author proposed the provisional reallocation of Merrill's species, on the basis of study of his figures and descriptions, to various dinoflagellate cyst genera (Sarjeant, 1964, p. 175).

Through the courtesy of Dr. H. B. Whittington, the author has been permitted to examine Merrill's type material, from the collections of the Museum of Comparative Zoology, Harvard. The results of this study are presented here.

STRATIGRAPHY AND MATERIAL

The specimens studied by Merrill were nodules of chert collected by Mr. Edward E. Cauthorne from "a quarry near Austin, Texas." They were obtained from the Caprina Chalk (now known as the Edwards Limestone), a member within the

Fredericksburg Formation, Comanchean Stage. This formation is considered to be equivalent to the middle and the lower part of the Upper Albian of Europe (Murray, 1961, p. 349).

The material in the Harvard collections consisted of three slides and seventeen partial nodules or slices of chert (MCZ 185A). Two of the three slides measure 2″ by 1″ and bear sections of flint cut to a thickness of between two and three times that of a normal petrological section (0.03 mm); these were unlabelled and are here referred to as slides I and II. The third slide consisted of a square of glass measuring 3″ by 2″ by ¼″ thick, bearing a wedge-shaped chert slice (varying in thickness from approximately eight times to approximately twice the thickness of a normal petrological section) which was surrounded by Canada balsam in an irregular ring. The shape of the balsam ring indicated that the chert slice had originally been fully twice its present size, but that one half had become detached and lost at some period. The thickness of the glass mount was too great to permit satisfactory examination; the surviving portion of chert was therefore remounted for study (slide III).

Merrill states that "several slides" were made from each nodule; it is therefore possible, in absence of any clear labelling, that the three surviving slides do not contain the holotype material of his species. As will be detailed later, a number of specimens showed a general correspondence to one or other of Merrill's figures, but the figures are unaccompanied by photographs and are not drawn with sufficient accuracy to permit any certain linking of specimen to figure. There remains a residue of figures which do not correspond even in a general fashion to any specimen located; it must be presumed in these cases, either that the holotypes were contained in other slides now lost, or that they were contained in the missing half of flint section III.

With Dr. Whittington's courteous permission, sections were made from the remaining chert specimens. Nine further mounts were made and examined (slides IV-XII); they were cut to a thickness of between three times and twice that of a normal petrological section. It was hoped that the lithological character would prove sufficiently variable to enable correlation of the new with the old slides and thus to link the latter to their source nodules; unfortunately, this did not prove possible, the sections showing insufficient distinctive features.

Merrill also mentions (p. 10) having made a comparative study of English cherts; three sections were made by Merrill, but these proved virtually barren of microorganisms and thus

cannot correspond to the surviving slides. Similarly, since English cherts are not mentioned on the specimen label, it must be assumed that the surviving chert specimens are entirely from Texas.

GENERAL DISCUSSION OF MERRILL'S RESULTS

The earliest studies of microfossils in chert flakes were made by C. G. Ehrenberg, in 1836; he assumed wrongly that the hystrichospheres were silicified and placed them in the freshwater desmid genus *Xanthidium*. The name "xanthidia" was used also in descriptions of similar fossils by a group of English microscopists, but G. A. Mantell conclusively demonstrated their organic rather than siliceous composition and thus precluded placing them in *Xanthidium* (1845).

Merrill was clearly unaware of these earlier studies and repeated Ehrenberg's error of assuming his microfossils to be silicified. He states (p. 8): ". . . we must suppose either that the spicules have been replaced by amorphous silica, or that they are still in the hyaline or colloidal state as found, and coloured yellow by some organic agent perhaps." He noted the presence in the cherts of foraminifera (rotaliids and textularids), either as "ghosts" entirely replaced by silica, or with the organic shell linings persisting; the latter he described as ". . . replaced by amorphous silica, the outlines remaining in a dark substance which has the appearance of an organic residue." This is one of several indications that Merrill was unaware of, or discounted, the possibility of structures formed of organic substances incorporated into the cherts and persisting almost unchanged. He effectively assumed the whole microfossil content of the chert sections to be originally siliceous or secondarily silicified. This attitude clearly orientated his thinking during his study, for, as will be shown in the ensuing section, the microfossils he described as sponge spicules include spores, pollen, hystrichospheres, wood and plant fragments, and even carbonate crystals.

Merrill noted the relatively low concentration of microfossils in the chert (p. 6): ". . . the number of organic remains is few, and the massive silica greatly in excess." This comment is wholly endorsed by the present author; the number of microfossils other than Foraminifera encountered in the nine new slides (IV-XII) averaged less than two. Foraminifera were comparatively abundant, averaging more than a dozen per slide.

DISCUSSION OF THE FORMS FIGURED BY MERRILL

In the presentation of his results, Merrill described the forms sequentially according to their arrangement in his plate (here reproduced as Text-fig. A). This procedure is again followed here: the numbers, and names given by Merrill (in quotes), are first stated, and a reinterpretation of the specimens follows.

1. and 2. "Monactinellid: *Axinella* ? sp." The figured specimens were not relocated; however, they appear to consist of sections through shell fragments which have been entirely replaced by silica. Merrill noted (p. 7) the finding of supposed shell fragments replaced by silica, but described them as a "bright transparent yellow" and thus was probably misinterpreting organic tissue fragments.

3. and 4. "Monactinellid: *Reniera* ? sp." Also probably oblique sections through shell fragments replaced by silica. The figured specimens were not positively relocated, but a number of similar fragments were noted.

5. "Monactinellid; acuate spicule." Neither description nor figure is sufficiently informative to permit either certain recognition of the figured specimen or precise determination of its true nature. However, it is most probably a fragment of organic tissue (?plant); such fragments are quite common in the cherts.

6. "Monactinellid." The figure and description support the presumption that this is a wood fragment; such fragments occur infrequently in the cherts.

7. "Monactinellid." Described by Merrill (p. 13) as "the most abundant of the sponge spicules found in the flint"; microorganisms of this type, varying considerably in the detail of size and shape, were encountered in all twelve cherts examined; the figure is not adequate to permit certain recognition of the holotype. The presence of septae crossing the cone at right angles to its long axis makes it probable that these are the shell linings of unilocular foraminifera (Pl. 1, fig. 1).

8. "Monactinellid." Also most probably a wood fragment; not relocated.

9. "Monactinellid: *Esperites* ? sp." Although stated by Merrill to be "a very common form" (p. 13), this figure was not correlated with certainty with any microstructure seen in the slides. It may possibly represent a replaced shell fragment or a fragment of organic tissue.

10. "Monactinellid: *Reniera* ? sp." Whilst neither figure nor description permit certainty, it is most probable that this represents a fragment of organic tissue (?plant). Plant fragments of similar appearance, some arcuate, were encountered with fair frequency.

11. "Tetractinellid: *Geodia ? austini* n. sp." This species was tentatively transferred to the genus *Systematophora* in an earlier paper (Sarjeant, 1964, p. 175). A specimen closely resembling the holotype is present in slide I (specimen IA: Pl. 1, fig. 10). From examination of both specimen and figure, there can be no question that this species is a junior synonym of *Hystrichosphaera ramosa* (Ehrenberg, 1838) O. Wetzel 1933, emend. Davey and Williams 1965a. The species name *austini* must therefore be rejected, under Article 63 of the "International Code of Botanical Nomenclature."

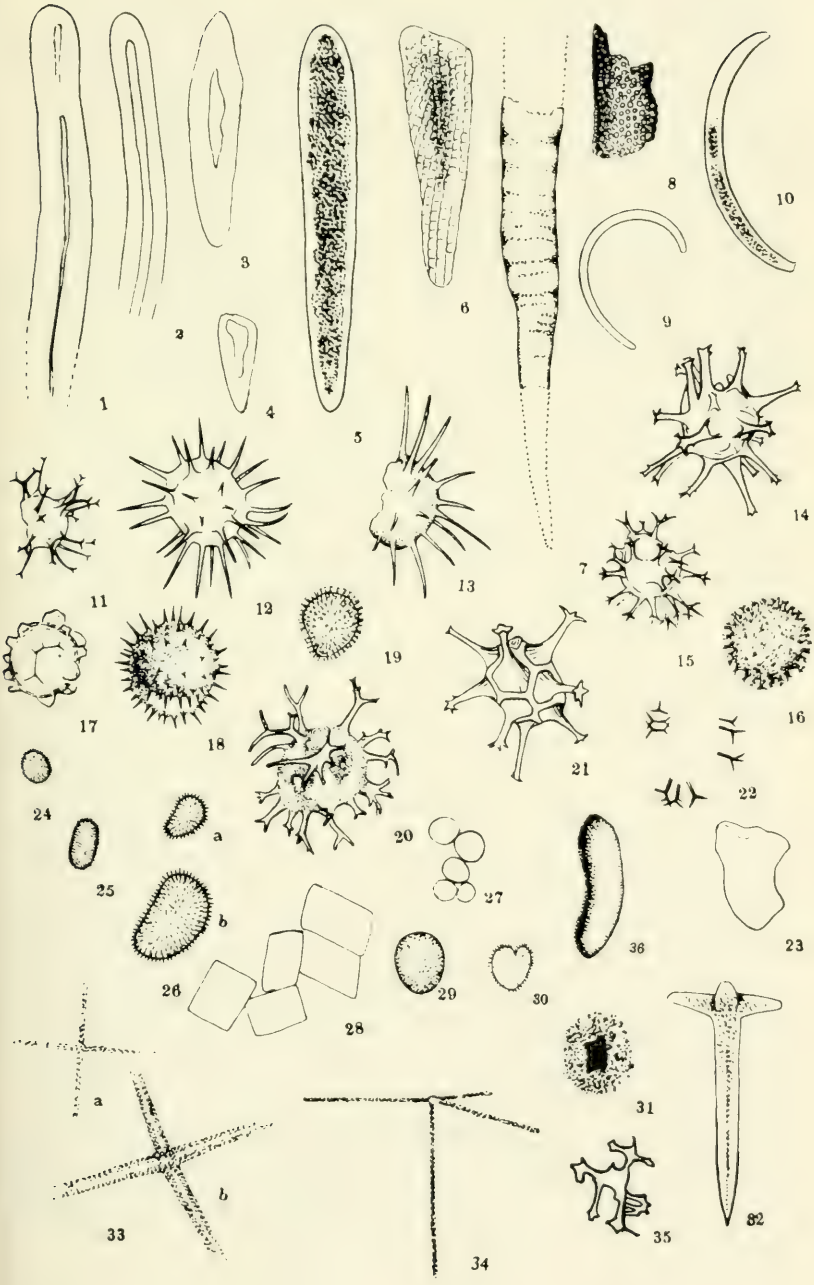
12. "Tetractinellid: *Geodia ? cretacea* n. sp." This species was transferred to the genus *Baltisphaeridium* in an earlier paper (Sarjeant, 1964). Several representatives of this species have been encountered in slide III. The holotype cannot be differentiated with complete certainty; the specimen most similar to the figure is specimen III J (Pl. 1, fig. 6). Hystrichospheres of this type are frequent in the Upper Cretaceous. Ehrenberg (1838) was the first to record such forms, applying the name *Xanthidium hirsutum*, which is that of a living desmid. Lejeune-Carpentier (1941) redescribed Ehrenberg's fossil material, under the name *Hystrichosphaeridium hirsutum*, but Deflandre (1946) correctly pointed out that the trivial name *hirsutum* could not be legitimately transferred to another genus and applied to the fossil forms. Deflandre had earlier (1937) proposed a new species *H. striolatum* for similar Upper Cretaceous forms having numerous slender, simple or branching spines, and a striate shell surface; there can be little doubt that Merrill's species *cretaceum* is a senior synonym of *striolatum*, although confirmation of the striate nature of the shell surface did not prove possible.

Under strict application of the rules of priority (Article 63 of the "International Code of Botanical Nomenclature") the name *cretaceum* is senior and should be retained; the name *striolatum* is junior and should be rejected. However, the species *striolatum* was soundly based, fully described and adequately figured; the species *cretaceum* was, in contrast, profoundly misinterpreted and inadequately figured and described. Moreover, complete certainty in the recognition of the holotype is not possible; and full

Text-figure A

A reproduction of Merrill's plate (1895). The specimens are here labelled according to the interpretation given in the present paper. Fuller discussions of the assignations are given in the text.

1-4.	Shell fragments sectioned at varying angles.
5.	A fragment of organic material.
6, 8.	Wood fragments.
7.	Shell lining of a unilocular foraminifer (?).
9.	Character not clear.
10.	Fragment of organic material.
11.	*Hystrichosphaera ramosa* (Ehrenberg, 1838).
12.	*Exochosphaeridium cretaceum* (Merrill, 1895) ≡ *E. striolatum* (Deflandre, 1937).
13.	*Hystrichodinium pulchrum* Deflandre (?).
14.	*Oligosphaeridium complex* (White, 1842).
15.	*Hystrichosphaera ramosa* (Ehrenberg, 1838).
16.	Spore.
17.	Character not clear.
18.	*Baltisphaeridium texanum* (Merrill, 1895).
19.	*Chlamydophorella* sp. (?).
20.	*Hystrichosphaera ramosa* (Ehrenberg, 1838).
21.	*Hystrichosphaeridium tubiferum* (H. H. White, 1842).
22.	Detached spines of *Hystrichosphaera ramosa* (Ehrenberg, 1838).
23–26.	Character not clear.
27.	"Brown bodies" of Bryozoa (?).
28.	Carbonate crystals.
29.	Dinoflagellate cyst, probably *Microdinium* sp. (?).
30, 31.	Character not clear.
32–34.	Probable sponge spicules.
35.	Fragment of *Hystrichosphaera ramosa* (Ehrenberg, 1838) (?).
36.	Fragment of organic material.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and accurate redescription of the holotype, even if certainly relocated, would not be possible because of the difficulty in studying chert-enclosed specimens at high magnification. The name *striolatum* is in widespread use; the name *cretaceum* has not been reused since its original publication, other than in taxonomic lists. Were a generic name concerned, an adequate case for conservation could be made under Article 14; unfortunately, this Article does not apply to species names. Nonetheless, it is here suggested that *striolatum* should continue to be used, in preference to the name *cretaceum*, in view of its more adequate description. The correct generic assignation is currently to *Exochosphaeridium* Davey, Downie, Sarjeant and Williams, 1966.

13. "Tetractinellid: *Geodia ? spini-curvata* n. sp." This species was transferred to the genus *Baltisphaeridium* in an earlier paper (Sarjeant, 1964, p. 175). No specimen comparable to the holotype or attributable, on grounds of general morphology, to this species, was encountered. The figure shows a form with relatively few, simple spines and having a precingular archaeopyle; it is probably referable to the genus *Hystrichodinium* Deflandre 1935 emend. Sarjeant 1965, perhaps to *H. pulchrum* Deflandre 1935, a species very frequent in English cherts. However, since the holotype is lost and since neither description nor figure permit certain statement of its characteristics, the species name *spini-curvatum* cannot continue in use.

14. "Tetractinellid: *Geodia ? irregularis* n. sp." This species was transferred to the genus *Hystrichosphaeridium* in an earlier paper (Sarjeant, 1964, p. 175). No specimen comparable to the holotype or attributable, on grounds of general morphology, to this species, was encountered. However, despite Merrill's statement (p. 15) that "Nothing similar to this has been found figured," there can be little doubt that this species is a junior synonym of *Oligosphaeridium complex* (H. H. White, 1842), Davey and Williams 1966a, a species frequent in the Cenomanian and known to range down well into the Lower Cretaceous.

15. "Tetractinellid: *Geodia ? tripunctata* n. sp." Rejection of this species on the grounds that it is a junior synonym of *Hystrichosphaera ramosa* (Ehrenberg, 1838) O. Wetzel 1933, emend. Davey and Williams 1966a, has already been proposed (Sarjeant, 1964, p. 175). A number of representatives of the species *H. ramosa* were encountered, including perhaps Merrill's holotype (specimen IIIC: Pl. 1, fig. 4); the earlier judgement is fully supported.

16. "Tetractinellid: *Hymeraphia* ? sp." The figured specimen was not found; however, Merrill's figure shows a trilete mark, indicating that his specimen was in all probability a spore. Spores and pollen occur infrequently in the chert sections; two somewhat similar forms are specimens IIIF (which resembles the figured specimens, but lacks a comparable clear trilete mark) and VIA (Pl. 1, fig. 5).

17. "Tetractinellid: *Chondrilla* ? sp." The figure and description of this form are so indefinite as to render impossible determination of its true character. One specimen encountered (IIC: Pl. 1, figs. 2, 3), a dinoflagellate cyst (questionably referable to the genus *Gonyaulacysta* and seen in oblique antapical view) may perhaps be Merrill's specimen, but this is incapable of confirmation.

18. "Tetractinellid: *Geodia? texana* n. sp." This species was transferred to the genus *Baltisphaeridium* in an earlier paper (Sarjeant, 1964, p. 175). Neither the holotype nor any comparable specimen was located; the morphology, as illustrated, is insufficiently characteristic to permit fuller comment on its probable affinities. Since the holotype is lost, a fuller analysis of the characteristics of the species is not possible; the name *texanum* cannot, therefore, continue in use.

19. "Tetractinellid: *Hymeraphia* ? sp." The figure is not especially informative, but shape, spine cover, and a faint indication of a cingulum combine to suggest a dinoflagellate cyst. The combination of characters strongly suggests a species of the genus *Chlamydophorella*; unfortunately, this probable assignation cannot be confirmed, since the figured specimen was not relocated.

20. "Tetractinellid: *Geodia? spinipansata* n. sp." This species was transferred to the genus *Hystrichosphaeridium* in an earlier paper (Sarjeant, 1964, p. 275). It is probable that a specimen encountered in slide III (specimen III B: Pl. 1, fig. 7) is the holotype. There can be no question that this is yet another specimen of *Hystrichosphaera ramosa* (Ehrenberg, 1838) O. Wetzel 1933, emend. Davey and Williams 1966a; this species shows some range of variation in morphology (cf. Davey and Williams, 1966a), and also varies in appearance according to orientation. The spines are not tubular, so that assignation to *Hystrichosphaeridium* is incorrect. The species *spinipansatum* must be rejected, as a junior synonym of *ramosa*.

21. "Tetractinellid: *Geodia? hilli* n. sp." This species was transferred to the genus *Hystrichosphaeridium* (Sarjeant, 1964). No specimen comparable to the holotype or attributable, on grounds of general morphology, to this species, was encountered. However, despite Merrill's repetition of his statement, earlier applied to No. 14, "Nothing similar has been found figured," the specimen he figures is without question attributable to the species *Hystrichosphaeridium tubiferum* (Ehrenberg, 1838) O. Wetzel 1933, emend. Davey and Williams 1966a, a species common throughout the Cenomanian and likely to be present in the Albian. The species *hilli* must, therefore, be rejected as a junior synonym of *tubiferum*.

22. "Tetractinellid: *Geodia tripunctata* ? n. sp. Fragments resulting from solution." Unquestionably these are detached spines of *Hystrichosphaera ramosa*. A number of such detached spines were seen, none corresponding precisely to the grouping shown in the figure, which might in any case be idealised.

23. "Lithistid ? Flesh spicule." This is described as "yellowish" and must be presumed to be a plant or wood fragment. The figure, by it generalised nature, precludes certain recognition; similar fragments were by no means uncommon.

24, 25, 26. "Tetractinellids; *Hymeraphia* ? sp." Over-simplified figures and descriptions again render certain recognition difficult. Pollen grains of comparable morphology were noted, and also (in slide X) a species of dinoflagellate cyst questionably attributable to the genus *Prolixosphaeridium* Davey, Downie, Sarjeant and Williams 1966, with a similarly elongate shape and cover of simple spines (Pl. 1, fig. 8).

27. "Tetractinellid: *Geodia* ? sp." Groups of circular, disc-like structures were encountered in several cherts (e.g. VII B; Pl. 1, fig. 11). Similar structures occur widely in palynological material from the Upper Mesozoic; Merrill's description (p. 17) is quite accurate. Their interpretation is doubtful; Otto Wetzel (1961, pl. 1, figs. 8-10) has figured similar forms as "brown bodies" of Bryozoa; it is also possible that they represent remains of colonial algae, possibly Chlorophyta.

28. "Tetractinellid: dermal spicules ?" These are abundant in most of the cherts examined and are undoubtedly rhomb-shaped carbonate (? dolomite) crystals. Carbonate crystals are frequently encountered in cherts and are sometimes considered to

indicate that the chert was formed by replacement of a pre-existing limestone. Merrill's misinterpretation of them is surprising (Pl. 1, fig. 12).

29. "Tetractinellid: *Geodia* sp." The figure may correspond to a specimen in slide III, which resembles it in general features (specimen IIIH). Although full study is difficult because of its situation deep in the chert, this is certainly a dinoflagellate cyst, and most probably a species of the genus *Microdinium*, species of which are known to occur in the Cenomanian.

30. "Tetractinellid: globo-stellate of dermal layer." This structure was not relocated and is of dubious reference, possibly pollen.

31. "*Geodia ?*" The figure and description are inadequate to permit recognition of this form.

32. "*Geodia* ? Pyramidal or zone spicule." Not relocated; most probably correctly interpreted as sponge spicules.

33, 34. "Hexactinellid. *Stauractinellia* ? sp." Not relocated; most probably correctly interpreted as sponge spicules.

35. "Frame work of a Hexactinellid?" This appears to be a fragment of a *Hystrichosphaera furcata*, although the figure is extremely generalised and precise interpretation is difficult. A similar fragment was encountered in slide III (specimen IIIE).

36. "Monactinellid: *Reniera* ? sp." The sausage-shaped object in Merrill's figure is most probably to be interpreted as a fragment of organic tissue (? plant); many similar fragments were seen.

CONCLUSIONS

A re-examination of Merrill's text and figures, in conjunction with study of the three surviving chert sections (one broken) and of new sections made from surviving fragments of cherts, makes it clear that, of the 36 microscopic structures he figures and describes, only three (none confirmed) can be regarded as representing sponge spicules. Nine of his figures certainly, and four others possibly, represent dinoflagellate cysts (mainly hystrichospheres); these include his eight proposed new species, of which five are junior synonyms of previously described species. The three remaining species retain technical validity, but the holotypes of two are lost, the descriptions and figures being insufficient to enable their accurate characterisation, and the holotype of the third species does not permit full study.

The remaining 20 microscopic structures figured and described by Merrill are of very diverse character. Four are considered to represent shell fragments sectioned in varying directions; one is thought to be a foraminiferal shell lining; one is a spore; three possibly pollen; one represents an association of disc-like structures, possibly "brown bodies" of Bryozoa; one comprises carbonate crystals; two represent wood fragments; four represent fragments of organic (? plant) tissue of varying shape; and three are of indeterminate character.

The currently valid species of dinoflagellate cysts recognised in Merrill's figures and material are *Hystrichosphaera furcata*, *Hystrichosphaeridium tubiferum*, *Exochosphaeridium striolatum*, *Oligosphaeridium complex*, *Hystrichodinium pulchrum* (doubtful), and undetermined species of the genera *Gonyaulacysta*, *Prolixosphaeridium*, *Hystrichodinium*, *Chlamydophorella* and *Microdinium*. Although the number of individuals encountered is small, and a full picture of the dinoflagellate cyst assemblage cannot be said to have been obtained, the species represented are all ones which would be likely to occur in Middle to Upper Albian preparations.

REFERENCES

Davey, R. J., C. Downie, W. A. S. Sarjeant and G. L. Williams

1966. Fossil dinoflagellate cysts attributable to *Baltispraeridium*. *In* Studies of Mesozoic and Cainozoic dinoflagellate cysts. Bull. Brit. Mus. (Nat. Hist.) Geol., Suppl. 3 (in press).

Davey, R. J. and G. L. Williams

1966a. The genera *Hystrichosphaera* and *Achomosphaera*. *In* Studies of Mesozoic and Cainozoic dinoflagellate cysts. Bull. Brit. Mus. (Nat. Hist.) Geol., Suppl. 3 (in press).

1966b. The genus *Hystrichosphaeridium* and its allies. *In* Studies of Mesozoic and Cainozoic dinoflagellate cysts. Bull. Brit. Mus. (Nat. Hist.) Geol., Suppl. 3 (in press).

Deflandre, G.

1935. Considérations biologiques sur les micro-organismes d'origine planctonique conservés dans les silex de la craie. Bull. Biol. Fr. Belg., vol. 69, pp. 213-44, pls. 5-9.

1937. Microfossiles des silex crétacés II. Ann. Paléont., vol. 26, pp. 51-103, pls. 8-18.

1946. Remarques sur la systématique des hystrichosphaeridés. C. R. Somm. Soc. Géol. Fr., No. 7, pp. 100-111.

EHRENBERG, C. G.

1838. Über das Massenverhaltnis der jetzt labenden Kieselinfusorien und über ein neues Infusorien-Conglomerat als Polierschiefer von Jastraba in Ungarn. Abh. K. Akad. Wiss. Berlin (1836), vol. 1, pp. 109-35, pl. 1.

GLAESSNER, M. F.

1945. Principles of micropalaeontology. Melbourne: University Press, 296 pp., 14 pls.

LEJEUNE-CARPENTIER, M.

1941. L'étude microscopique des silex (9 ième note). Sur *Hystrichosphaeridium hirsutum* (Ehr.) et quelques formes voisines. Ann. Soc. Géol. Belg., vol. 63, no. 3, pp. 71-92.

MANTELL, G. A.

1845. Notes of a microscopical examination of the Chalk and Flint of southeast England. Ann. Mag. Nat. Hist., vol. 16, no. 103, pp. 73-88.

MERRILL, J. A.

1895. Fossil sponges of the flint nodules in the Lower Cretaceous of Texas. Bull. Mus. Comp. Zool., Harvard. (Geology Ser. III), vol. 28, no. 1, pp. 1-26, 1 pl.

MURRAY, G. E.

1961. Geology of the Atlantic and Gulf Coastal Province of North America. New York: Harper, 692 pp.

SARJEANT, W. A. S.

1964. Taxonomic notes on hystrichospheres and acritarchs. J. Paleont., vol. 38, pp. 173-7.

1966. Dinoflagellate cysts with a *Gonyaulax* type tabulation. *In* Studies of Mesozoic and Cainozoic dinoflagellate cysts. Bull. Brit. Mus. (Nat. Hist.) Geol., Suppl. 3. (in press).

WETZEL, O.

1933. Die in organischer Substanz erhaltenen Mikrofossilien des Baltischen Kreide-Feuersteins. Palaeontographica, vol. 77, pp. 141-88; vol. 78, pp. 1-110, pls. 1-7.

1961. New microfossils from Baltic Cretaceous flintstones. Micropalaeontology, vol. 7, no. 3, pp. 337-50, pls. 1-3.

WHITE, H. H.

1842. On fossil Xanthidia. Microsc. J., vol. 11, pp. 35-40, pl. 4.

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Plate 1

Fig. 1. Presumed shell lining of a unilocular Foraminifer (Fig. 7 "Monactinellid" of Merrill). × 500.

Figs. 2, 3. *Gonyaulacysta* sp. indet., seen in oblique apical view (Fig. 2) and, by transparency, in oblique antapical view (Fig. 3) — the antapex is at left. Figure 2 closely resembles "Tetractinellid; *Chondrilla* ? sp." of Merrill. × 500.

Fig. 4. *Hystrichosphaera ramosa* (Ehrenberg). The presumed holotype of Merrill's invalid species *Geodia ? tripunctata.* × 500.

Fig. 5. *Hystrichosphaera ramosa* (Ehrenberg). Possibly the holotype of Merrill's invalid species *Geodia ? spini-pansata.* × 500.

Fig. 6. *Exochosphaeridium cretaceum* (Merrill). The specimen may be the holotype. × 500.

Fig. 7. *Hystrichosphaera ramosa* (Ehrenberg). A specimen in terminal view, illustrating the high degree of variation in appearance given by orientation. × 500.

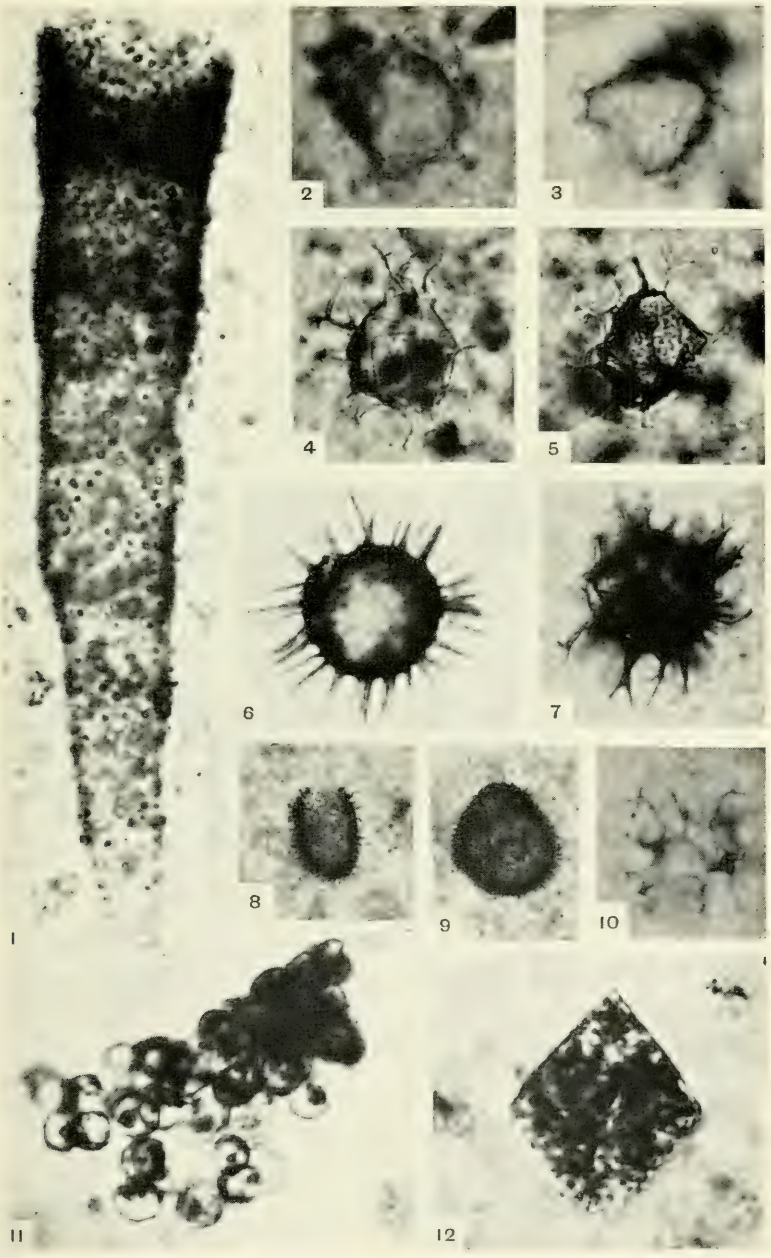
Fig. 8. *Prolixosphaeridium* sp. indet. (Possibly corresponding to Merrill's Fig. 26b "Tetractinellid; *Hymeraphia* ? sp."). × c300.

Fig. 9. Spore, gen. et sp. indet. (Similar to Merrill's Fig. 16 "Tetractinellid; *Hymeraphia* ? sp."; but lacking a clear trilete mark.) × c300.

Fig. 10. *Hystrichosphaera ramosa* (Ehrenberg). Possibly the holotype of Merrill's invalid species *Geodia ? austini.* × 500.

Fig. 11. Group of disc-like organisms, possibly "brown bodies" of Bryozoa (equivalent to Merrill's Fig. 27 "Tetractinellid; *Geodia* ? sp."). × 500.

Fig. 12. A carbonate (? dolomite) crystal. Similar crystals are described by Merrill as "Tetractinellid: dermal spicules?" × 500.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Museum of Comparative Zoology

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QUATERNARY FISH FOSSILS FROM WEST OF LAKE RUDOLF, KENYA

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INTRODUCTION

The fossils to be described in this paper were collected during the summer of 1963 by a party from the Museum of Comparative Zoology, consisting of Professor Bryan Patterson, Messrs. A. D. Lewis, C. T. Williams, and the author. It is a pleasure to acknowledge the assistance given to us by Dr. L. S. B. Leakey, and by Mr. John Walsh of the Mines and Geological Department, Kenya, who called our attention to the deposits discussed in this paper.

The late Pleistocene and Quaternary deposits west of Lake Rudolf, North Kenya (Turkana District), were visited by us during a survey of the Miocene formations in the region. Accounts of earlier visits to the region are given by Arambourg (e.g. 1943), and Fuchs (1939). A general view of the area concerned is shown in the accompanying map. A range of hills (including Losidok) west of the lakeshore is Tertiary in age, consisting of grits and volcanics. Along the base of this range there are exposed large and extensive beds of Pleistocene age — largely unfossiliferous lake beds, including conglomerates of small clay pebbles with, in places, small rocks derived from the volcanics. Away from the bases of the hills — and here we explored only eastwards — are flat plains covered with gravel and windblown sands; close to the lake large sand dunes occur. These plains extend from the hills down to the lakeshore. Nearer the lake, as Fuchs has noted (1939), there is evidence of at least two former beaches, some 220 and 90 feet above the current level of the lake. Along these beaches fossils may be found on the surface, although their derivation is difficult to determine, and "reefs" of the

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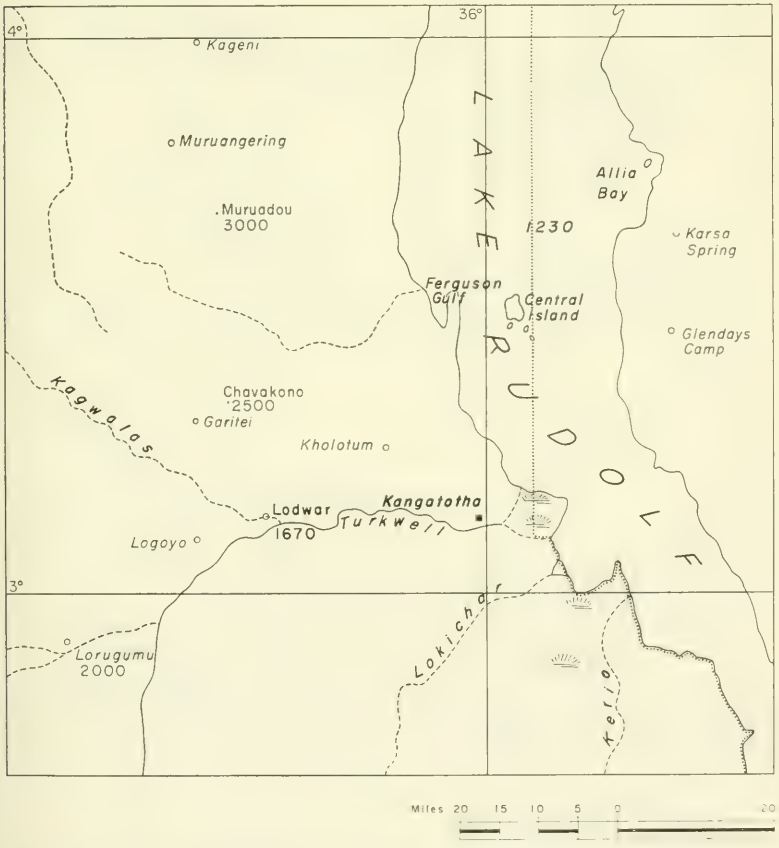
freshwater oyster, *Aetheria elliptica,* also occur. We were able to follow the beaches for several miles and found fossils even down to the lakeshore. In several places drainage from the plains has cut into the deposits and we found a number of large gullies or washes along the sides of which the bedding of the deposits — apparently with a slight eastward dip — was visible, and fossils could be collected *in situ.* The principal place from which fossils were collected was an extensive exposure at Kangatotha (see map), where the Turkwell River has made a large cut through some hundred feet of the lake deposits. Patterson and Williams measured the exposed section as follows:

Upper unit, bed	10	Surface	white sands
"	9	4 feet	black clay
"	8	16 feet	white coarse sands with gravel lenses
"	7	2½ feet	grey clay
"	6	10 feet	micaceous sand
"	5	4 feet	black clay
"	4	½ to 5 feet	coarse sand and gravel
"	3	5 feet	black clay
		¾ foot	white sand
		2½ feet	black clay
"	2	9 feet	interbedded black clays and grey sands
"	1	12 feet	black clays
Lower unit, bed	5	7 feet	fine grey sand
"	4	3½ feet	fine grey sand highly indurated with iron
"	3	5 feet	fine white sands, black micaceous flakes
"	2	4 feet	medium yellow sands, black micaceous flakes
"	1	12½ feet	coarse grey sands with large clay pebbles in upper unit (base concealed)

"Upper unit" and "lower unit" are informal, non-committal terms; formal stratigraphic naming should follow, not precede, a general survey of the Lake Rudolf Quaternary. The two units are readily distinguishable, the upper being predominantly dark in colour, the lower light. Slightly indurated fillings of plant roots are abundant in the lower unit.

Partly due to the swollen state of the river and partly due to lack of time, a similar cliff on the south bank of the watercourse, here about half a mile wide, was not visited. The tip of northern cliffs corresponds to the 220 foot level of Fuchs.

Mollusc, fish, reptilian and mammalian remains are common in the upper unit of the exposures, mollusc and fish in the lower. A human skull, a partial mandible, and various skeletal fragments were found isolated in bed 8 of the upper unit, and poorly preserved parts of a human skeleton were found in the overlying black clay of bed 9. Artifacts and pottery fragments are common on the surface and both were encountered *in situ* in bed 7 of the upper unit.



Sketch map of Lake Rudolf and the Lodwar region (Turkana District, Kenya) showing position of the Kangatotha locality.

FOSSIL FISHES

All the fish remains collected consisted of isolated bones, never associated, and very often fragmentary. Few showed great signs of weathering or of having been "rolled." The bones were highly mineralized, often showing considerable iron content, despite their relatively recent age (see below).

From lower to upper strata, the fish were distributed as follows:

Lower unit, base of bed 5, seven feet below junction with upper unit
- Order Ostariophysi
  - Suborder Siluroidea
    - Family Mochokidae
      - *Synodontis* sp.
        - Seven pectoral spine fragments
    - Family Clariidae
      - *Clarias* sp.
        - One articular (posterior portion), one quadrate (articular portion)
  - Suborder Cyprinoidea
    - Family Cyprinidae
      - cf. *Barbus*
        - Two dorsal pterygiophore fragments
- Order Percomorphi
  - Suborder Percoidea
    - Family Centropomidae
      - *Lates* cf. *Lates niloticus* Cuvier and Valenciennes
        - One incomplete parasphenoid (length 150 mm), three vertebrae (diam. 25, 33, 46 mm), four fin spines (38, 52, 55, 62 mm)
    - Family Cichlidae
      - *Tilapia* sp.
        - Two fragments of pterygiophores, six fin spines (2 nearly complete, 55 and 47 mm), two branched fin rays, and one vertebra

Lower unit, bed 5 (general)
Order Ostariophysi
Suborder Cyprinoidea
Family Cyprinidae
cf. *Barbus*
Tentatively referred to this genus are sections of two fin spines.

Order Percomorphi
Suborder Percoidea
Family Centropomidae
Lates cf. *Lates niloticus* Cuvier and Valenciennes
Four dorsal fin spines (28, 42, 45, 51 mm)

Family Cichlidae
Tilapia sp.
One pterygiophore — first interhaemal (70 mm), two dorsal fin spines (incomplete), four vertebrae: two abdominal (diam. 10, 11 mm), one caudal (diam. 15 mm), one terminal (diam. 8 mm, length 26 mm)

Upper unit, bed 5
Order Ostariophysi
Suborder Siluroidea
Family Bagridae
Bagrus cf. *Bagrus bayad* (Geoffroy)
Posterodorsal portion of a single occiput (estimated height 28-30 mm)

Family Mochokidae
Synodontis cf. *Synodontis schall* Cuvier
Humeral process of left cleithrum (49 mm long), one posttemporal bone, and fragments of four pectoral spines

Family Clariidae
Clarias cf. *Clarias lazera* Cuvier and Valenciennes
Posterior portion of dermethmoid bone (breadth 25 mm), median portion of supraoccipital (max. breadth 35 mm) and eleven vertebrae (diam. 8, 12, 13, 13, 13, 15, 15, 16, 17, 17, 17 mm)

Suborder Cyprinoidea
Family Cyprinidae
Barbus cf. *Barbus bynni* Cuvier and Valenciennes
Three dorsal pterygiophores (incomplete), one pharyngeal (length approx. 37 mm), one vertebra (diam. 6 mm)

Order Percomorphi
Suborder Percoidea
Family Centropomidae
Lates cf. *Lates niloticus* Cuvier and Valenciennes
The most abundant fish in this unit; twenty-three vertebrae (diam. 12, 13, 16, 19, 20, 20, 24, 25, 26, 26, 26, 27, 27, 30, 34, 35, 35, 37, 42, 42, 50, 51, 53 mm), the articular regions of four quadrates, one incomplete preoperculum, four incomplete fin spines, three fragments of hyomandibulars, one dermethmoid, one partial parasphenoid, two left premaxillae (proximal ends), one maxilla (distal end), and two isolated neural arches (probably from anterior vertebrae)

Family Cichlidae
Tilapia sp.
One dorsal pterygiophore, two spines, nine vertebrae (diam. 8, 7, 6, 6, 6, 6, 5, 5, 5 mm)

Upper unit, bed 8
Order Ostariophysi
Suborder Siluroidea
Family Mochokidae
Synodontis cf. *Synodontis schall* Cuvier.
The humeral process of one cleithrum (length 55 mm), one dorsal fin spine, three pectoral fin spine fragments

cf. *Synodontis*
Fragments of three spines

Family Clariidae

Clarias cf. *Clarias lazera* Cuvier and Valenciennes

Three dermethmoids (2 complete, lengths 34, 45 mm; one incomplete, anterior width 50 mm), one posttemporal, two sections of supraoccipital (one anterior, one posterior), one pectoral fin spine fragment, two vertebrae (diam. 13, 19 mm)

Suborder Siluroidea indet.

One vertebra (diam. 23 mm), two dorsal fin spines (80, 48 mm) and several spine fragments

Suborder Cyprinoidea

Family Cyprinidae

Barbus cf. *Barbus bynni* Cuvier and Valenciennes

Four pharyngeal bones (approx. length 30, 30, 40, 45 mm), two (?dorsal) pterygiophore fragments

cf. *Barbus*

Two vertebrae (diam. 14, 15 mm)

Order Percomorphi

Suborder Percoidea

Family Centropomidae

Lates cf. *Lates niloticus* Cuvier and Valenciennes

Six articular bones (posterior sections), five incomplete quadrates (articular sections), four incomplete preoperculars, the proximal ends of five premaxillae, the anterior part of one right palatine, one dermethmoid, five dorsal fin spines, twenty-two vertebrae (1 second vertebra — diam. 25 mm; 3 third vertebrae — diam. 20, 23, 27 mm; 18 abdominal vertebrae — diam. 17, 20, 20, 20, 22, 24, 24, 28, 28, 28, 29, 29, 32, 33, 34, 40, 48, 49 mm), plus a number of shattered and unidentifiable fragments of large cranial elements

Upper unit, bed uncertain

These fishes were collected at one of the smaller exposures near the lake shore, about two miles north of the mouth of the Turkwell.

Order Ostariophysi
Suborder Siluroidea
Family Bagridae
Bagrus cf. *Bagrus bayad* (Geoffroy)
One occiput, incomplete (max. depth 69 mm)

?Family Clariidae
Dermethmoid portion of skull, incomplete

Order Percomorphi
Suborder Percoidea
Family Centropomidae
Lates cf. *Lates niloticus* Cuvier and Valenciennes
Posterior portion of a skull (depth of occipital region 80 mm), one premaxilla (length 127 mm), three vertebrae (diam. 29, 30, 88 mm). Note the extreme size of these specimens.

Collected on lake shore, horizon not known, but probably upper unit
Order Percomorphi
Family Centropomidae
Lates cf. *Lates niloticus* Cuvier and Valenciennes
Eight vertebrae (diam. 14, 18, 20, 24, 25, 26, 27, 30 mm) and three dorsal fin spines (40, 44, 46 mm)

Family Cichlidae
Tilapia sp.
One incomplete fin spine

DISCUSSION

Of the living species to which the fossils are most closely comparable — *Bagrus bayad*, *Synodontis schall*, *Clarias lazera*, *Lates niloticus*, *Barbus bynni*, and *Tilapia nilotica* — only *Bagrus bayad*, according to Worthington and Riccardo (1936), does not

frequent sheltered or shallow waters. *Synodontis schall* is distributed universally in Lake Rudolph. With the possible exception of the bigger *Tilapia* and *Lates*, the others are confined to the sheltered and shallower areas of the lake, such as, for example, Ferguson's Gulf. A tentative conclusion from examination of the fossils would therefore be that bed 5 of the upper unit was laid down in more open and less shallow waters than bed 8 of this unit or the upper bed of the lower unit.

An interesting feature of the fish fauna is the very great size of the largest vertebra of *Lates* from the fifth locality (lakeshore, horizon uncertain); this is far larger than is known from present-day *Lates*. Daget (1959) and White (1926) have described similar giant Quaternary *Lates*, and it is interesting to discover that such forms were still extant in such relatively very recent times, as shown in these Rudolf materials.

The nature of the fish fauna does not afford any direct evidence as to the age of the Kangatotha beds, since the Nilotic nature of the Rudolf fish fauna has been stable at least since the Lower Pleistocene disconnection of the lake basin from the Nile drainage (see Fuchs, 1939, for general chronology of the area). The mammalian fauna, so far as studied, is of Recent aspect.

The Kangatotha beds belong to the very latest stage in the history of the Rudolf basin. Their level and position would suggest that they were laid down while the lake was at its largest extent after the Gamblian Pluvial, presumably during the Makalian or Nakuran "wet phases" (see Cooke, 1957, 1963). A radio-carbon date of 4,800 ± 100 years was obtained from a sample of *Etheria elliptica* from the "beaches" on the lake shore, noted above. This attests to very recent age of the deposits and implies an extremely rapid fossilization. It is of great interest to note that the giant forms of *Lates*, described by Daget, White, and in this paper, survived to a very recent date. Finally, with respect to the time scale, a note may be added here about one of the artifacts collected on the surface of bed 7 of the upper unit. This is a uniserially barbed bone harpoon (now in the Peabody Museum, Harvard University). De Heinzelin (1957) lists the distribution of similar harpoons and gives a scheme of the evolution of harpoon design with an estimate of the equivalent culture. (To de Heinzelin's list should be added a specimen from the late Upper Kenya Capsian of Gamble's Cave described by Oakley, 1961). At first view, the Kangatotha harpoon seems to resemble the penultimate stages of design as shown by specimens from the "S.F.M." and "G.Y." levels at Ishango (de Heinzelin, 1957),

whereas the "N. tuff." specimens from Ishango, the specimen found by Arambourg (1943) at Nanoropus near the end of Lake Rudolf, and the Gamble's Cave specimen are of a more advanced style.

ACKNOWLEDGMENTS

The expedition was financed by NSF Grant No. GP 1188. In addition to the acknowledgment made in the introduction, it is a pleasure to thank Dr. P. H. Greenwood for his enthusiastic assistance in the study of the material and Professor Bryan Patterson for valuable comments on the manuscript and for providing the sketch map (Fig. 1).

LITERATURE CITED

Arambourg, C.

1943. Mission Scientifique de l'Omo 1932-1933. Tome 1. Géologie-Anthropologie. Fasc. II. Mus. Nat. Hist. Natur. (Paris). Pp. 1-74.

Cooke, H. B. S.

1957. Observations relating to Quaternary environments in east and southern Africa. Trans. Geol. Soc. S. Africa, **60** (Annex.), 73 pp.

1963. Pleistocene mammal faunas of Africa, with particular reference to southern Africa. Pp. 65-116 *in* F. C. Howell and F. Bourlière, eds., African Ecology and Human Evolution. Aldine Co., Chicago.

Daget, J.

1959. Restes de poissons du Quaternaire saharien. Bull. Inst. Franc. Afr. Noire, **23**: 182-191.

De Heinzelin, J.

1957. Les feuilles d'Ishango. Exploration du Parc Albert, 1957: 46-61.

Fuchs, V. E.

1939. The geological history of the Lake Rudolf basin, Kenya Colony. Phil. Trans. Roy. Soc. London, (B) **229**: 219-274.

Oakley, K. P.

1961. Bone harpoon from Gamble's Cave, Kenya. Antiq. J., **41**: 86-87.

White, E. I.

1926. The geology and paleontology of the Kaiso bone-beds. Part II. Palaeontology. Fossil Pisces. Occas. Paper Geol. Surv. Uganda, **2**: 45-51.

Worthington, E. B. and C. K. Ricardo

1936. Scientific results of the Cambridge expedition to the East African lakes, 1930-1, no. 15. The fish of Lake Rudolph and Lake Baringo. J. Linn. Soc. London, Zool., **39**: 353-389.

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B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS. APRIL 29, 1966 NUMBER 244

A NEW SPECIES OF *ASHMUNELLA* FROM WEST TEXAS (MOLLUSCA: PULMONATA)

BY W. J. CLENCH AND W. B. MILLER[1]

The first specimens of this new species were collected by our colleague, Dr. J. C. Bequaert, in the Davis Mountains, West Texas, in May and September 1961. All of the specimens were dead shells. During June 1965 live specimens of this species were collected by Dr. J. C. Bequaert and W. B. Miller from which the anatomical drawings were made by the junior author.

ASHMUNELLA BEQUAERTI new species

Plate 1; text figures 1, 2

Holotype: MCZ 260274, taken from a rockslide about ¼ mile up a tributary canyon (locally known as Goat Cave Canyon) to Little Aguja Canyon near Buffalo Trail Boy Scout Camp at the base of the northeastern slope of Black Mountain in the Davis Mountains, Jeff Davis County, Texas. Elevation 4,900 ft. (J. C. Bequaert and W. B. Miller, 5 June 1965).

Igneous rockslides line both sides of the canyon, below vertical cliffs; *Ashmunella bequaerti* was found on both sides of the canyon, at elevations from 4800 ft. to 4900 ft., along with *Humboldtiana palmeri* Clench and Rehder, in association with *Quercus texana, Q. hypoleucoides, Acer grandidentata and Rhus trilobata.*

[1] University of Arizona, Dept. of Zoology.

Paratypes: MCZ 260275 from the same locality.

Height mm	Greater Diameter mm	Lesser Diameter mm	
3.9	12.2	11.5	Holotype
3.8	13.0	11.7	Paratype
3.7	12.4	11.0	"
3.8	12.2	11.1	"
3.5	11.7	10.5	"
3.4	11.3	10.1	"
3.2	10.7	9.5	"
3.0	10.5	9.3	"

Description: Shell lenticular, slightly convex above, moderately convex below, acutely carinate, widely umbilicate, thin, pale brown. The surface, above and below and into the umbilicus, is sculptured with fine growth wrinkle-striae from which project numerous cuticular scales giving a pilose appearance to fresh clean shells; the scales also extend well into the umbilicus. In live and recently dead animals, the scales usually hold dirt and debris, giving a dusty, dirty appearance to the surface. In older specimens where the scales have worn off, there remain raised hyphen-shaped papillae, parallel to the growth striae, giving a granular appearance to the surface. There are six whorls, the first half whorl of the embryonic shell glossy with only a few incipient radial striae, the remainder with a silken appearance, the fine growth wrinkle-striae and the papillae and scales. The first two and a half whorls are convex; subsequent whorls flattened. Last whorl descends slightly to the aperture and is deeply guttered close behind the outer and basal margins of the lip. The under surface of the body whorl is marked additionally by very fine, microscopic, spiral striae. The aperture is small and very oblique; peristome white to light brown, reflected except near the upper insertion of the lip, the terminations connected by a slightly raised callus. Parietal wall with two teeth, the larger one situated basally, sinuous, diverging posteriorly toward the smaller upper one, thicker anteriorly; the smaller one close to the upper insertion of the lip, raised posteriorly. Outer margin thickened, with a flat-topped rectangular tooth set transversely across the aperture, spanning and overlapping the gap between the parietal teeth. On the basal margin, two longitudinally compressed teeth are connected by a raised ridge along the peristome. Interdental intervals are about equal. The umbilicus,

measured from lower suture of body whorl just behind peristome to opposite side of body whorl in the pit, is contained about four times in the greater diameter of the shell.

The mantle over the lung is clear except for rare, very small groups of light grey pigment spots.

Jaw with ten ribs.

Genitalia. Penis with lower sac short and wide, upper sac longer and narrower. In the upper sac there are three longitudinal ridges, in addition to a small nodule which is attached to the wall of the penis at its junction with the epiphallus. In whole mounts, this nodule gives the appearance of a short verge when seen by transparency; dissection of the penis, however, reveals it as a growth on the side of the penial wall. It is possible that this nodule, together with the tip of the muscular walls of the epiphallus, acts as a papilla when the penis is completely everted. The lower sac has two thickened processes which come together near the lower end and form a constriction within the penial cavity. There is a short penial retractor on the epiphallus which is inserted in the floor of the lung cavity; loose strands of connective tissue connect the penis with base of epiphallus. Talon of the multilobar type. Length of penis 5.0 mm, epiphallus 24.0 mm, flagellum 1.5 mm, penial retractor 1.3 mm, spermatheca and duct 31.0 mm, vagina 4.0 mm, free oviduct 2.5 mm, atrium 1.0 mm.

Remarks: Ashmunella bequaerti is the most easterly known species of *Ashmunella* in the U. S. It is most closely related to the *mearnsi* group, in shell characteristics as well as geographically. In paratypes, the spire varies from moderately raised conical to completely flat; the diameter varies from 10.5 mm to 13.0 mm. Its nearest relative appears to be *A. hebardi* Pilsbry and Vanatta, with which it agrees in the lenticular shape of the shell, the sharply carinate periphery, and the general shape of the teeth, including the two parietal teeth. In *A. bequaerti*, however, the shell is generally more flattened, the edge of the parietal callus is appressed and very weak, not raised into a low, free ridge as in *hebardi*, and the upper insertion of the peristome is only weakly descending, nearly straight, not strongly descending as in *hebardi*. Anatomically, the internal nodule at the upper end of the upper penial sac has not been seen or reported in any other *Ashmunella*. It remains to be seen from additional dissections, however, whether this is a consistent characteristic.

The new species is named after Dr. Joseph C. Bequaert, lifelong malacologist and entomologist, who first discovered this

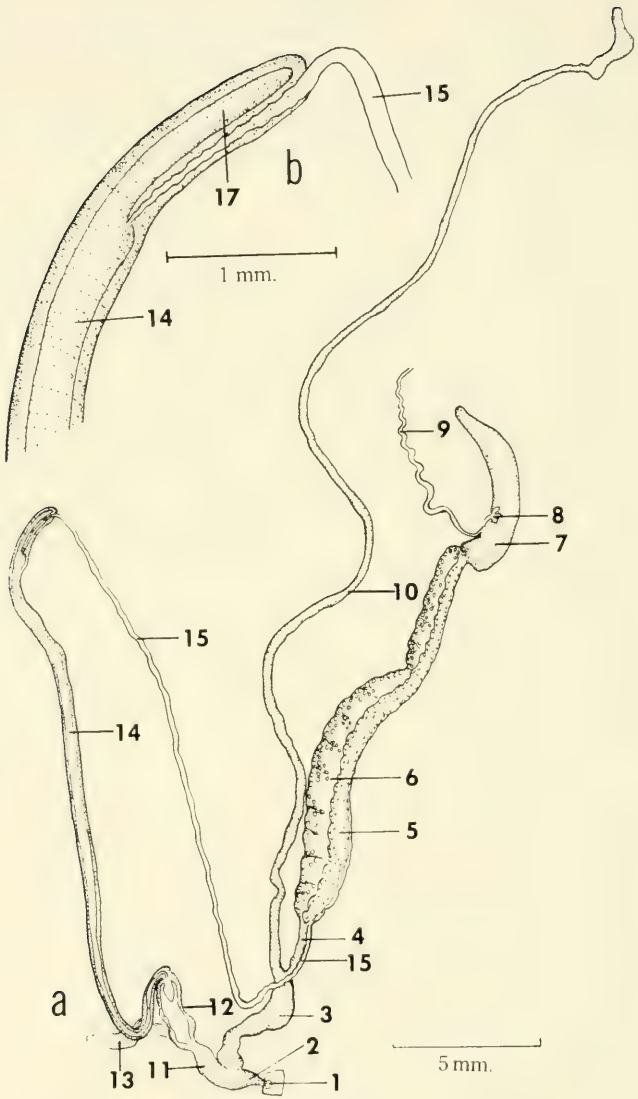


FIG. 1. *Ashmunella bequaerti* Clench and Miller. Dissection of reproductive system with illustrations made from stained whole mount. *a*, Entire system. *b*, Enlargement of the distal end of the epiphallus at its junction with the vas deferens where the two are bound together. This may be called the flagellum portion of the epiphallus. There is no free flagellum.

1, Genital orifice; 2, Atrium; 3, Vagina; 4, Oviduct; 5, Prostate; 6, Uterus; 7, Albumen gland; 8, Talon; 9, Hermaphroditic duct; 10, Spermathecal duct; 11, Lower sac of penis; 12, Upper sac of penis; 13, Penial retractor; 14, Epiphallus; 15, Vas deferens; 16, Connective tissue; 17, Flagellum bound with vas deferens; 18, Penis papilla.

snail on 2 May 1961, obtaining quantities of dead shells but no live animals. On 5 June 1965, he and the junior author returned to the locality and were successful in obtaining 4 live adults and 3 live immatures. Dead shells were very numerous. One of the live adults was designated the holotype. Two others were dissected to corroborate anatomical findings. The fourth live adult and the three live immatures are being kept alive in a terrarium at the University of Arizona, in the hope of obtaining additional studies on the adult anatomy for comparison.

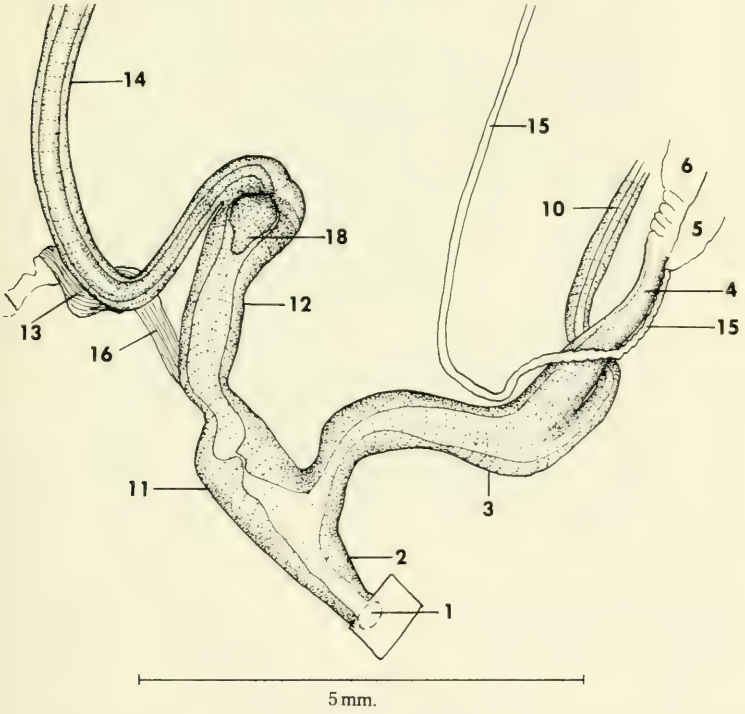


FIG. 2. *Ashmunella bequaerti* Clench and Miller. Lower portion of reproductive system enlarged. (Numbering as in Figure 1.)

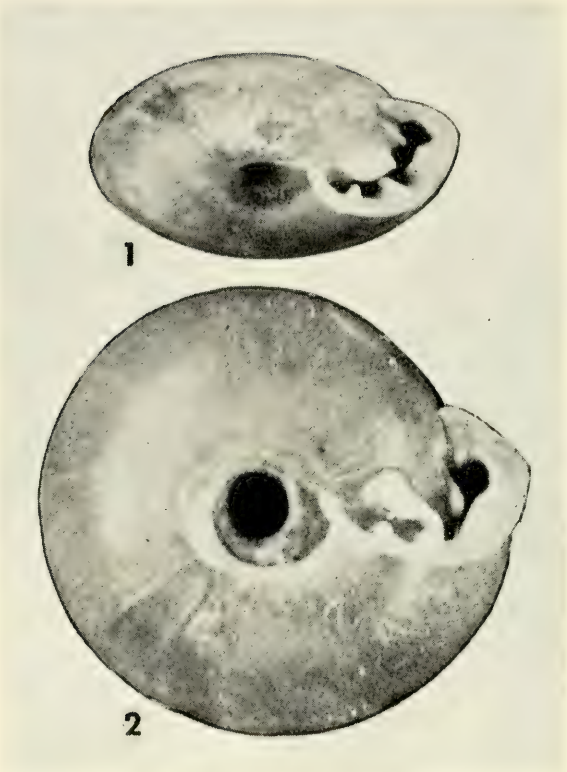
REFERENCES

PILSBRY, H. A.

1940. Land Mollusca of North America. Academy of Natural Sciences, Philadelphia, Monograph No. 3, vol. 1, pt. 2, pp. 912-977.

1948. The genera *Humboldtiana*, *Sonorella*, *Oreohelix* and *Ashmunella*. Proc. Acad. Nat. Sci., Philadelphia, vol. **100**, pp. 199-203.

(Received 24 January, 1965.)



FIGS. 1-2. *Ashmunella bequaerti* Clench and Miller, from Goat Cave Canyon, Black Mt., Davis Mts., Texas. Fig. 1. Paratype, MCZ 260275 (4 X). Fig. 2. Holotype, MCZ 260274 (5.4 X).

BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. APRIL 29, 1966 NUMBER 245

NOTES AND DESCRIPTIONS OF NEW UROCOPTIDAE FROM CUBA AND HISPANIOLA (MOLLUSCA: PULMONATA)

BY WILLIAM J. CLENCH

The following notes and descriptions of new species are based upon material in the Museum of Comparative Zoology which has been collected over the past several years. All species are members of the family Urocoptidae, one of the most dominant families in the West Indies and in a lesser way in Central America and in the southwestern United States. This family occurs also in northern South America, but species are few and present only a very minor element in the molluscan fauna there.

UROCOPTIDAE

ARCHEGOCOPTIS Pilsbry

Archegocoptis Pilsbry, 1903, Manual of Conchology (2) **15**:301 (type species, *Cylindrella crenata* Weinland and Martens, original designation).

So far as known, this genus is confined to the southwestern or Tiburon Peninsula of Haiti. Specific localities for the few species are all from the Département du Sud.

According to Pilsbry, *Archegocoptis* is nearest in relationship to *Eucalodium* Crosse and Fischer, a genus limited in distribution to southern Mexico and Guatemala.

The known species are as follows:

ARCHEGOCOPTIS BARBOURI Clench

Archegocoptis barbouri Clench, 1935, Proc. Boston Soc. Nat. Hist. **41**:5, pl. 1, figs. B, F (Tardieu, Mt. LaHotte, Haiti, ± 3000 feet). [Holotype, MCZ 108593.]

Archegocoptis crenata (Weinland and Martens)

Cylindrella crenata Weinland and Martens, 1859, Malakozoologische Blätter **6**:54 (Jérémie, Haiti); Pfeiffer, 1869, Novitates Conchologicae **3**:440, pl. 97, figs. 33, 34 (Haiti).

Archegocoptis darlingtoni Clench

Archegocoptis darlingtoni Clench, 1935, Proc. Boston Soc. Nat. Hist. **41**:6, pl. 1, figs. C, G (Tardieu, Mt. LaHotte, Haiti, ± 3000 feet). [Holotype, MCZ 108592.]

Archegocoptis decapitata (Röding)

Cerion decapitatum Röding, 1798, Museum Boltenianum, p. 90 (no locality given [Haiti]). [See below.]

Archegocoptis eximia (Pfeiffer)

Cylindrella eximia Pfeiffer, 1857, Malakozoologische Blätter **4**:232 (locality unknown); Pfeiffer, 1869, Novitates Conchologicae **3**:439, pl. 97, figs. 30-32 (Haiti).

Archegocoptis tiburonica Clench

Archegocoptis tiburonica Clench, 1935, Proc. Boston Soc. Nat. Hist. **41**:6, pl. 1, fig. I. (Tardieu, Mt. LaHotte, Haiti, between 3-4000 feet). [Holotype, MCZ 108591.]

Archegocoptis haitiensis new species

Plate 1, figures 1, 2

Holotype. MCZ 252056, from the top of Morne Rochelois, 25 km WSW of Miragoane, Dépt. du Sud, Haiti, about 3000 feet, collected by W. J. Eyerdam, July 1927.

Paratypes. A series of 5 paratypes from the same locality, MCZ 252057.

Height mm	Width mm	
41	10	Holotype (see Remarks)
27	10	Paratype
26.5	10	"
26.5	10	"

Description. Shell medium in size, reaching 42+ mm in length (decollated), minutely umbilicate and coarsely sculptured.

Color a more or less uniform chocolate-brown and shining on the coarse, axial riblets and dull in between. Whorls 15+ and flat sided. Suture well defined. Spire extended, the upper portion slightly concave. Aperture holostomatous, subcircular, slightly flaring and reflected. Axis simple. Sculpture consisting of a series of somewhat irregular axial costae which are diagonal and fine, irregular axial threads in between the costae. There is a well defined basal ridge.

Remarks. In relationship, this species is nearest to *Archegocoptis tiburonica* Clench, differing, however, by being much larger, lacking the whorl shoulder and in having a much larger basal ridge. The sculpture is similar in both species, though coarser in *A. tiburonica.*

Many species in the family Urocoptidae lose many of the upper whorls when approaching the adult stage or during their adult life. They produce a plug in one of the mid or earlier whorls and later the whorls above the plug are lost. The fracture is a mechanical one and not automatic, as quite frequently a few adult specimens in a single population may still retain their early whorls. It is of considerable interest to note that *A. haitiensis* apparently does this twice, as three of the five paratypes have plugs seven whorls above the aperture; the remaining two paratypes are young specimens and have lost the early three or four whorls. Only the holotype has retained the mid-whorls.

Archegocoptis decapitata (Röding)

Cerion decapitatum Röding, 1798, Museum Boltenianum, p. 90 (refers to Chemnitz, 1786, Conchylien-Cabinet (1)**9**: pl. 136, figs. 1256-1257 [fig. 1255, in error]).

Cyclostoma fasciata Lamarck, 1816, Encyclopédie Méthodique, Atlas, p. 12, pl. 461, fig. 7.

Helix truncata Dillwyn, 1817, Descriptive Catalogue of Recent Shells, London **2**:948 (Santo Domingo).

Helix fasciata Lamarck: Férussac, 1822, Tableaux Systématiques, p. 61, no. 503 (The Antilles).

Cylindrella fasciata 'Chemnitz' Pfeiffer, 1862, Malakozoologische Blätter **9**:199 (Corail [Haiti]).

Cylindrella fasciata 'Chemnitz' Crosse, 1891, Jour. de Conch. **39**:134 (Corail, near Jérémie, SW Haiti).

Urocoptis truncata (Dillwyn): Pilsbry, 1903, Manual of Conchology (2)**15**:154, pl. 39, figs. 27-28 (Corail, near Jérémie, Haiti).

Cyclostoma fasciata Lamarck: Mermod, 1952, Revue Suisse de Zoologie **59**:46, fig. 111.

Remarks. This species has had a long and varied history. The only specific locality previously known was that of Weinland who had collected a single worn specimen in a small water course at Corail, Haiti (Crosse, 1891). From this, Pilsbry had assumed that it had been carried down this stream from the mountains above. In 1927, W. J. Eyerdam collected several dead specimens under stones at the base of a cliff in a forested area on Grande Cayemite, a small island about 6½ miles NE of Corail. It is possible that the specimen found by Weinland may have drifted from Grande Cayemite. The specimens collected by Eyerdam are certainly in the genus *Archegocoptis* and appear to be *A. decapitata* Röding, differing only in that the color band of dull red is on a whorl lower than those figured by both Chemnitz and Lamarck. All specimens so far as known were collected dead.

Urocoptis (Gongylostoma) whittumi new species

Plate 2, figure 1

Holotype. MCZ 59580, from Guabairo, near Soledad, Cienfuegos, Las Villas, Cuba, collected by Clench, Crozier and Navez, October 1928.

Paratypes. MCZ 59284, 86289, 105148, all from the above locality, and collected by various students and visitors to the Harvard Tropical Gardens.

Height mm	Width mm	
11.5	2.7	Paratype
11.6	2.5	"
14.8	3	"
16	3	"
17.3	3.2	Holotype
17.5	3	Paratype
18.5	3	"
20.5	3.5	"

Description. Shell somewhat fusiform, usually decollated, narrow, widest point a little below the middle in the decollated specimens. Color very pale reddish brown, darker on the earlier whorls. Whorls 18 to 22 (not always decollated at the same whorl). Whorls rather flat, evenly tapering towards the spire tip. Last whorl free for one-quarter to one-third of its length. Spire acute, first two whorls a little larger than the third and fourth. Aperture holostomatous, circular, white and reflected.

Columellar axis stout, encircled by a single, wide lamella which bears numerous deep, spine-like crenulations. Sculptured by numerous strong, almost straight riblets, about 17-18 on the second whorl.

Remarks. This species belongs to the group of *U. canteroiana,* but differs in having fewer and stronger riblets, different shape and proportions, and by its internal axis, which is stouter; it is also encircled by a larger lamella, the margin of which possesses a greater number of tooth-like processes.

This shell is very variable in size, but very constant in its relative proportions. The riblets are approximately the same in number on the different sizes.

Named for Mr. Walter Whittum, now of Springfield, Massachusetts, whose kindness and courtesy made many trips possible in the rich collecting ground about Guabairo, at the time he was in charge of a colonia for the Soledad Sugar Company in 1928.

Urocoptis (Gongylostoma) exquisita new species

Plate 2, figure 2

Holotype. MCZ 59286, from one-half mile E of Guabairo, Soledad, Cienfuegos, Cuba, W. J. Clench collector, December 1927.

Paratypes. MCZ 59285, 59579, from the same locality.

Entire specimens Height mm		Decollated specimens Height mm
14.4	Holotype	12.7
14.4		12.5
12.9		11.9

Description. Shell fusiform, slender, generally entire; when decollated, limited to only a very few of the early whorls. Widest point about midway in decollated shells. Color light horn, not uniform, but generally somewhat marbled with patches of lighter and darker areas, occasionally albinistic; surface somewhat glistening, often translucent in certain areas. Whorls convex, evenly tapering towards both the spire tip and the aperture. In complete shells whorls number 21-23; in decollated specimens 15-18 whorls. Spire acute, first two whorls slightly larger than the third and fourth. Last whorl free, developed with a long, slightly curved neck. Aperture holostomatous, circular, white and well reflected.

Axis of columella thin and sinuous with a single spiral thread. Suture somewhat impressed. Sculpture consisting of very fine oblique axial riblets except on the free whorl which has many relatively coarse riblets, irregularly spaced and nearly encircling the whorl except on the face or aperture side.

Remarks. This species belongs in the subgenus *Gongylostoma* Albers, near *Urocoptis barbouri* Torre and Clench. It differs from *U. barbouri,* however, in being smaller, and with a larger number of whorls in the decollated specimens, and is relatively more slender and more fusiform. The color is very similar, though the shell is a little more translucent in *exquisita.* The free aperture whorl is also much longer than in *U. barbouri.*

The habitat of this species is quite peculiar for the genus in this region, as specimens were found in more or less heavy woods, on the rocky walls of cave entrances, or in other large rocky fissures. The other urocoptids occupied more open areas, especially *U. livida barbouri* and *U. livida atkinsi* Torre and Clench.

Urocoptis (Gongylostoma) canteroiana (Arango)

Plate 2, figure 4

Cylindrella canteroiana 'Gundlach' Arango, 1875 [1876], Anales Real Academia Ciencias Medicas, Fisicas y Naturales, Habana **12**:284 (La Vigía, Trinidad [Cuba]); Arango, 1878, Fauna Malacologica Cubana, Habana, p. 117 (environs of Vigía, Trinidad).

Urocoptis canteroiana 'Gundlach' Arango: Pilsbry, 1903, Manual of Conchology (2)**15**:254.

Height mm	Width mm	
12.5	2.5	Lectotype

Lectotype. Here selected, MCZ 189252, from La Vigía, Trinidad, Cuba, collected by Gundlach and sent to MCZ by Rafael Arango.

Remarks. This species has not been figured previously. It is comparatively rare as only a few specimens have been collected. We have specimens from La Vigía, Finca Cantero, and Finca La Pastora, all in the vicinity of Trinidad, Las Villas, Cuba.

Urocoptis (Gongylostoma) diagonalis new species

Plate 2, figure 3

Holotype. MCZ 59292, from Mina Carlota, Sierra de San Juan, 8 miles S of Cumanayagua, Las Villas, Cuba, W. J. Clench and Calvin Goodrich collectors, November 30, 1927.

Paratype. A single paratype from the same locality is in the Museum of Zoology, University of Michigan.

Height mm	Width mm	
16	3.3	Holotype
15	3	Paratype

Description. Shell reaching 16 mm in height (decollated), fusiform, imperforate and sculptured. Color a dull gray. Whorls 16 (remaining), very slightly convex, the last free for about one-fifth of a whorl. Suture indented. Spire decollated, a loss of 12-14 early whorls. Aperture holostomatous, white and flaring. Sculpture consisting of numerous fine, axial riblets which are slightly diagonal and are flatly sigmoid in shape. On the free portion of the last whorl these riblets become rings and are closer together.

Remarks. This species is related to *U. canteroiana* (Arango), but differs in several of its characters. *U. diagonalis* is larger, has finer sculpture of diagonal riblets which are straight in *canteroiana* and flattened sigmoid in shape in *diagonalis.*

Urocoptis (Urocoptola) cayemitensis new species

Plate 1, figure 4

Holotype. MCZ 254666, from NE Grande Cayemite, a small island about 6½ miles NE of Corail, Département du Sud, Haiti, collected by W. J. Eyerdam, July 1927.

Paratypes. MCZ 254667, population 1; and MCZ 254668, population 2. From the same locality as the holotype.

Height mm	Width mm		
17.2	6.5	Holotype,	population no. 1[1]
18.5	7	Paratype	"
17.3	5.8	"	"
15.8	6	"	"
20.5	7.1	"	population no. 2[1]
20.4	7	"	"
20.1	7	"	"

Description. Shell oblong, glossy, having the greatest diameter above the middle, imperforate, sculptured and rather thin in structure. Color a pale brownish pink. Whorls very slightly

[1] Both populations from the same general area.

convex and tapering above the mid-whorls to the truncated summit. Last whorl with a distinct basal ridge. Spire extended. Aperture nearly circular, the parietal area adnate to the whorl above, lip flaring. Suture moderately impressed. Sculpture consisting of numerous, slightly diagonal, axial costae, which do not produce crenulations at the suture. Axis with a single twist.

Remarks. This species is a member of the *U. sericea* (Pfeiffer) complex which is widely distributed along coastal Haiti within the Gulf of Gonave. *Urocoptis cayemitensis* differs from *U. sericea* by being much smaller, imperforate, and in having a uniform sculpture throughout. The spire is truncated between the seventh and eighth whorls from the aperture.

Urocoptis (Urocoptola) ekmani new species

Plate 1, figure 5

Holotype. MCZ 260871, from La Source, NW Gonave Island, Haiti, collected by W. J. Eyerdam, August 1927.

Paratypes. MCZ 260872, from the locality of the holotype.

Height mm	Width mm	
25	11	Holotype
26	11	Paratype
22.5	10.2	"

Description. Shell large, elliptical in shape, remaining whorls reaching 26 mm in height, imperforate, rather solid and sculptured. Whorls 8 (remaining) and moderately convex. Flesh colored with a few, small, irregular, dark brownish red flecks on all of the whorls. Spire extended and tapering rapidly from the mid-area and produced at an angle of about 55°. Aperture subcircular, holostomatous, one specimen out of eight being adnate above. There is a slight and closed rimation at the umbilical area. Suture slightly indented. Sculpture consists of diagonal and straight, fine axial riblets on the upper whorls and diagonal and arcuate axial riblets on the lower whorls. Protoconch unknown.

Remarks. This species is related to *Urocoptis bencomoi* Clench, but is smaller, proportionally narrower, and has the lip holostomatous.

Named for Dr. Erik L. Ekman, the Swedish botanist who was with W. J. Eyerdam during his trip to Gonave Island.

Urocoptis (Urocoptola) caribbaea new species

Plate 1, figure 3

Holotype. MCZ 260873, from 1 mile E of Pointe à Raquette, south central Gonave Island, Haiti, collected by W. J. Eyerdam, July 1927.

Paratypes. MCZ 260874, from the same locality.

Height mm	Width mm	
24.8	12	Holotype
22	11.6	Paratype
22.5	11	"
22.5	11.4	"

Description. Shell large, reaching about 25 mm in height, imperforate, rather solid and sculptured. Whorls 7 (remaining) and moderately convex. Flesh colored with a few small, irregular, dark brownish red flecks on all of the whorls. Spire extended and tapering to the apex and the base from the mid-area and produced at an angle of about 60°. Aperture subcircular and adnate on the parietal area. Suture slightly indented. Sculpture consists of diagonal and straight, fine axial riblets and somewhat arcuate on the last whorl. Riblets on the two remaining early whorls more widely spaced. Protoconch unknown.

Remarks. This species is closely related to *U. ekmani*, differing in being shorter, with different proportions, having all specimens adnate on the parietal area and in having the axial riblets more widely spaced on the remaining early whorls.

Urocoptis (Idiostemma) perplicata (Beck)

Helix (*Cochlodina*) *perplicata* Férussac, 1821 [1822], Tableaux Systématiques Animaux Mollusques, p. 61 or 65, no. 506 (The Antilles) [*nomen nudum*].

Brachypodella perplicata Férussac: Beck, 1837, Index Molluscorum, p. 89 [refers to Férussac's pl. 163, fig. 9].

Clausilia perplicata Férussac: Deshayes [*in*] Lamarck, 1838, Animaux sans Vertèbres (2)**8**:216.

Cylindrella perplicata Férussac: Philippi, 1847, Abbildungen Conchylien **2**:217, pl. I (Achatina), fig. 9 (The Antilles).

Cylindrella perplicata Férussac, 1851, Histoire Naturelle Générale et Particulière **2**:229, pl. 163, fig. 9 (The Antilles); non *Cylindrella perplicata* Férussac. Pfeiffer 1840 [*in*] Weigmann, Archiv für Naturgeschicte **1**:41 (Fundador, Matanzas, Cuba).

Cylindrella fastigiata 'Gundlach' Pfeiffer, 1860, Malakozoologische Blätter **7**:20 (Baracoa, Mata, and Yunque, Cuba); Pfeiffer, 1865, Novitates Conchologicae **2**:263, pl. 65, figs. 23-25 [Syntypes, MCZ 26639, 86621].

Urocoptis fastigiata Pfeiffer: Pilsbry, 1903, Manual of Conchology (2)**15**:171, pl. 45, figs. 36-41 (Baracoa, El Yunque, Mata, Oriente, Cuba).

Brachypodella perplicata Férussac: Pilsbry, 1903, Manual of Conchology (2) **16**:83, pl. 7, figs. 23-24 (Antilles).

Remarks. Considerable confusion has existed concerning the proper name for this species. Pilsbry retained both *perplicata* and *fastigiata* in two different genera but noted under *perplicata* that "the ribs follow one another from whorl to whorl, as in *Urocoptis fastigiata*," but he gave no indication that the two names applied to the same species.

Since Pilsbry's Manual of Conchology was published in 1903 far more material in this family is available for study, not only from Cuba but from the entire West Indies as well.

The credit for the name of this species must go to Beck rather than to Férussac, as Férussac did not publish this name until 1851. The plates were issued much earlier but there were no names attached to them. Through some source, other than publication, these names were available, and Beck was the first to cite a plate and figure for this species.

Specimens examined. CUBA: Oriente, Farallones de Barigua; Yunque de Baracoa; Silla de Báez, W of Baracoa; Sabana, Cabo Maisi; Zona de la Caleta, Baracoa; Arriba Mandinga, Baracoa; Arriba Guandao, Mandinga; Mata, Punta Maisi; Boca de Taco, Nibujon, Baracoa.

Brachypodella (Brevipedella) imitatrix Pilsbry

Brachypodella (*Brevipedella*) *imitatrix* Pilsbry, 1903, Manual of Conchology (2)**16**:47, pl. 8, figs. 54-55 (Port-au-Prince, Sans-Souci, St. Marc, and La Ferrière, Haiti).

Remarks. This species has a much wider distribution than most species in the Urocoptidae, extending as it does from Haiti to the Samaná peninsula in eastern Santo Domingo.

A closely related species, *B. angulifera* (Gundlach), occurs in eastern Cuba.

Specimens examined. Haiti: Bizonton, Lasbaines; Port-au-Prince and Diquini. Santo Domingo: Mt. Isabel de Torres, Puerto Plata, at 1200 to 1600 feet; Sanchez; Peñon de Basiles and Peñon de Maria Luisa, both Santa Bárbara de Samaná, and Punta Lirio, 2 miles E of Santa Bárbara de Samaná.

Brachypodella (Gyraxis) samana new species

Plate 2, figure 5

Holotype. MCZ 57214, from Peñon de Maria Luisa, Santa Bárbara de Samaná, República Dominicana, collected by W. J. Clench, H. D. Russell and R. A. McLean, August 1937.

Paratypes. MCZ 57218, from the same locality; and MCZ 57213 from Peñon de Basiles in the same general area.

Height mm	Width mm	
14.5	2.5	Holotype
12.5	2.4	Paratype
14.5	2.5	"
12.8	2.4	"

Description. Shell slender, imperforate, generally entire, widest at the mid-section of the shell and finely sculptured. Color marbled in yellowish and light brown with some areas white, the brownish areas translucent, the white and yellowish areas somewhat opaque. Whorls 13 to 14 in entire specimens and moderately convex with the last whorl free. Suture well defined. Spire acute, aperture holostomatous, subcircular with the lip flaring slightly. Axis gyrate. Sculpture consisting of numerous, fine, axial, slightly diagonal and slightly curved costae; the first two whorls finely and axially costate. On the early whorls certain of these costae in small groups impinge slightly on the suture.

Remarks. This species is closely related to *Brachypodella (Gyraxis) sericata* Pilsbry. It differs by being larger, having slightly coarser thread-like costae and having the marbled coloration, *sericata* being a dull white.

Brachypodella sericata Pilsbry was collected originally by William M. Gabb during 1869-71 while on a geological survey of Santo Domingo. Unfortunately, the recent mollusks collected by him seldom had specific locality data. We collected this species in some numbers at San Lorenzo Bay, Bahía de Samaná. This locality can be considered the type locality as Gabb surveyed this area about the Bahía de Samaná.

(Received December 1, 1965.)

Plate 1

FIGS. 1-2. *Archegocoptis haitiensis* n. sp. Morne Rochelois, 25 km WSW of Miragoane, Dépt. du Sud, Haiti, at 1000 meters. Fig. 1, Paratype, MCZ 252057; fig. 2, Holotype, MCZ 252056 (both 3X).

FIG. 3. *Urocoptis* (*Urocoptola*) *caribbaea* n. sp. 1 mile E of Pte. à Raquette, S central Gonave Island, Haiti. Holotype, MCZ 260873 (3X).

FIG. 4. *Urocoptis* (*Urocoptola*) *cayemitensis* n. sp. NE Grande Cayemite, Dépt. du Sud, Haiti. Holotype, MCZ 254666 (4X).

FIG. 5. *Urocoptis* (*Urocoptola*) *ekmani* n. sp. La Source, NW Gonave Island, Haiti. Holotype, MCZ 260871 (3X).

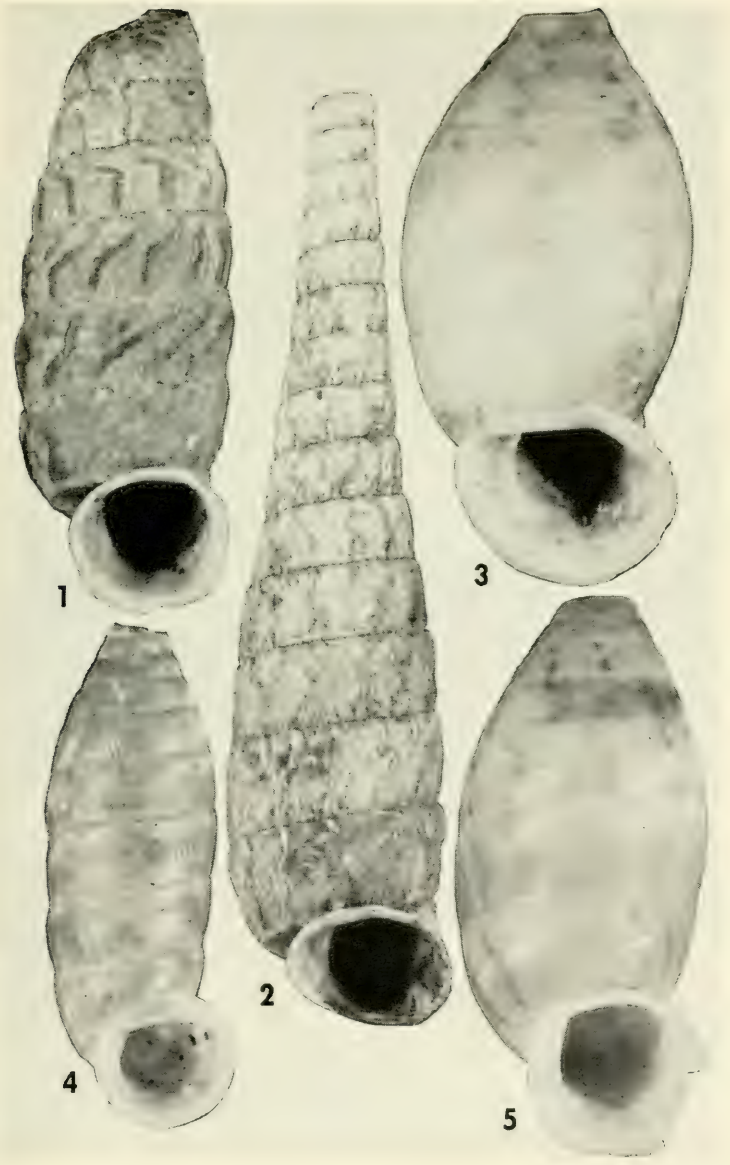


PLATE 1

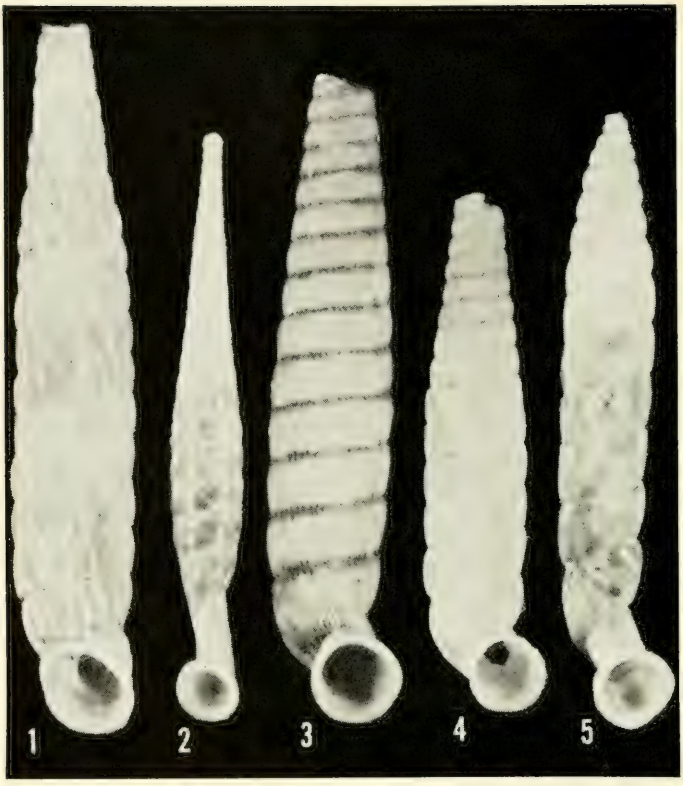


Plate 2

Fig. 1. *Urocoptis* (*Gongylostoma*) *whittumi* n. sp. Guabairo, Soledad, Las Villas, Cuba. Holotype, MCZ 59580 (5.5 X).

Fig. 2. *Urocoptis* (*Gongylostoma*) *exquisita*, n. sp. ½ mile E of Guabairo, Soledad, Las Villas, Cuba. Holotype, MCZ 59286 (5.5 X).

Fig. 3. *Urocoptis* (*Gongylostoma*) *diagonalis* n. sp. Mina Carlota, Sierra de San Juan, 8 miles S of Cumanayagua, Las Villas, Cuba. Holotype, MCZ 59292 (5.5 X).

Fig. 4. *Urocoptis* (*Gongylostoma*) *canteroiana* (Arango). (La Vigía, Trinidad [Las Villas, Cuba]). Lectotype, MCZ 189252 (5.5 X).

Fig. 5. *Brachypodella* (*Gyraxis*) *samana* n. sp. Peñon de Maria Luisa, Santa Bárbara de Samaná, República Dominicana. Holotype, MCZ 57214 (5.5 X).

BREVIORA

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PSEUDANTHESSIUS PROCURRENS N.SP., A CYCLOPOID COPEPOD ASSOCIATED WITH A CIDARID ECHINOID IN MADAGASCAR

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and

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INTRODUCTION

During an extensive search in 1963-64 for copepods associated with marine invertebrates at Nosy Bé, in northwestern Madagascar, 109 adults and 9 copepodids of the new lichomolgid copepod described below were recovered from the sediment obtained after washing 30 large pencil urchins, *Phyllacanthus imperialis* (Lamarck), in weakly alcoholized sea water. (The host echinoid is widespread in the Indo-Pacific region, where it occurs, for example, in Australia, the Marshall Islands, the Philippine Islands, Ceylon, the Red Sea, and Zanzibar). This new form brings the total number of species known in the genus *Pseudanthessius* to 24 (including the 22 species listed by Stock, Humes, and Gooding, 1963, and a new species from a polychaete annelid in Madagascar whose description by Humes and Ho is in press).

ACKNOWLEDGMENTS

The copepods were collected by the author while participating in the 1963-64 activities of the U.S. Program in Biology of the International Indian Ocean Expedition.

The study of the specimens has been aided by a grant (GB-1809) from the National Science Foundation of the United States.

I wish to thank Dr. H. Barraclough Fell, Professor of Invertebrate Zoology at the Museum of Comparative Zoology, for the identification of the echinoid host, and to acknowledge the assistance to the field work given by the staff of the Centre d'Océanographie et des Pêches at Nosy Bé.

DESCRIPTION

Family LICHOMOLGIDAE Kossmann, 1877

Genus Pseudanthessius Claus, 1889

Pseudanthessius procurrens[1] n.sp.

Figures 1-29

Type material. — 16 females, 9 males, and 1 copepodid from washings of 3 pencil urchins, *Phyllacanthus imperialis* (Lamarck), in 1 meter depth among dead coral (*Acropora*) at Pte. Ambarionaomby, Nosy Komba, near Nosy Bé, Madagascar. Collected November 28, 1963. Holotype female, allotype, and 19 paratypes (13 females and 6 males) deposited in the U. S. National Museum, Washington, and the remaining paratypic adults (dissected) together with the copepodid in the collection of the author.

Other specimens (all from *Phyllacanthus imperialis* collected in 1963 at the type locality). — 2 females from 1 host, July 3; 10 females and 7 males from 3 hosts, July 18; 14 females and 5 males from 6 hosts, August 23; 13 females, 6 males, and 4 copepodids from 7 hosts, October 30; and 16 females, 11 males, and 4 copepodids from 10 hosts, December 14. This last collection is deposited in the Museum of Comparative Zoology.

Female. — The body (Figs. 1 and 2) has a broadened prosome. The length (excluding the setae on the caudal rami) is 0.95 mm (0.90-1.01 mm) and the greatest width is 0.44 mm (0.42-0.46 mm), based on 10 specimens. The ratio of the length to the width of the prosome is 1.28:1. The segment bearing leg 1 is almost completely fused with the head, the only indication of separation being a short weak crease on each side. The lateral areas of the metasomal segments are rounded.

The segment of leg 5 (Fig. 3) is expanded laterally, being 50 μ in length and 133 μ in width. Between the segment of leg 5 and the genital segment there is a ventral intersegmental sclerite (see Fig. 2). The genital segment (Fig. 3) is 127 μ long. Anteriorly its lateral margins form 2 rounded, strongly sclerotized lobes (the width of the segment at this level being 115 μ). The width at the level of the dorsolateral areas of attachment of the egg sacs is 107 μ. Behind each attachment area the segment is slightly

[1] The specific name *procurrens*, from Latin *procurrere*, meaning to bulge out or project, alludes to the outer expansion on the coxa of leg 1 and to the 2 rounded lobes on the anterior part of the genital segment in the female.

constricted with nearly parallel margins (the width in this region being 86 μ). Each egg sac attachment area (Fig. 4) bears anteriorly a slender, slightly haired seta (21 μ long) and just posterior to it a short naked seta (6.5 μ long) composed of an expanded sclerotized basal portion and a slender hyaline distal part. Medial to the latter seta there are 2 small spinelike processes. The three postgenital segments are 44 x 81, 39 x 75, and 65 x 72 μ from anterior to posterior. The anal segment bears on each side on its distal margin a dorsal and ventral row of spinules.

The caudal ramus (Fig. 5) is elongated, with a terminal ventral expansion whose margin bears a row of spinules. The length along the inner side of the ramus to the end of the expansion is 114 μ, along the outer side 104 μ, and the width at the level of the outer seta is 24 μ. The ratio of length to width is about 4.5:1. The outer seta, inserted 70 μ from the base of the ramus, is naked and 56 μ in length. The pedicellate dorsal seta is 33 μ and slightly haired. The outermost terminal seta (100 μ) and the innermost terminal seta (72 μ) are haired. The 2 long median terminal setae are 177 and 250 μ in length respectively and haired. A minute lateral setule is borne on the outer basal margin of the ramus. The dorsal and ventral surfaces of the ramus bear a few refractile points.

The dorsal surface of the prosome and the dorsal and ventral surfaces of the urosome bear minute setules and refractile points. In addition, the outer ventral areas of the head carry a submarginal row of refractile points (Fig. 6). The ratio of the length of the prosome to that of the urosome is 1.53:1.

The egg sacs (Fig. 1) are moderately elongated, often rather pointed posteriorly, and contain numerous eggs. In one female the egg sacs measured 385 x 220 μ, with each egg about 57-60 μ in diameter.

The rostral area (Fig. 7) is moderately well developed. Between this area and the front of the labral region there is a slight protrusion on the ventral surface of the head.

The first antenna (Fig. 8) is 7-segmented, with the lengths of the segments (measured along their posterior non-setiferous margins) 24 (39 μ along the anterior margin), 103, 21, 39, 33, 20, and 17 μ respectively. The formula for the armature is 4, 13, 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. All the setae are naked.

The second antenna (Fig. 9) is 4-segmented, with the last segment elongated (69 μ along the shorter ventral margin, 93 μ along

the dorsal margin, and 19 μ in width). Each of the first two segments bears a small ventral seta, the third segment bears 4 slender setae (one of them very small), and the last segment bears 2 unequal slender recurved claws (47 and 25 μ respectively along their axes) and 5 setae, one of them very long (99 μ). The extremity of the last segment is swollen, so that the 2 claws insert at one side rather than directly on the tip of the segment. All the setae are naked.

The labrum (Fig. 10) consists of 2 diverging, pointed lobes with their medial edges straight and finely dentate, both arising from a large, conspicuous, sclerotized area which projects (Fig. 2) from the ventral surface of the head. On the posterior wall of the labrum, in front of the mouth area, there is a pair of small sclerotized lobes. The surface of the labrum lacks fine ornamentation.

The mandible (Fig. 11) has on the concave side of the blade an oblique row of spinules followed distally by a spinelike process lying parallel to the blade and evidently not articulated with it. The convex side of the blade bears a fringe of graduated spinuliform structures without definite articulations. The paragnath (Fig. 12), lying medial to the base of the first maxilla (as in Fig. 16), is a rounded lobe bearing a small sclerotized outer process, a small postero-inner knob, and a posterior group of hairs. The first maxilla (Fig. 13) is a single segment bearing 4 naked elements, comprising terminally 2 obtuse subequal spines (10 and 8 μ long) and a shorter pointed spine (5 μ) and subterminally a naked hyaline seta (11 μ). The second maxilla (Fig. 14) is 2-segmented. The first segment is unarmed but has a small sclerotized protuberance on its expanded margin. The second segment is produced to form a long bilaterally spinulose lash; the dorsal surface bears a proximal seta 29 μ in length (bearing lateral spinules along one edge) and a distal row of 3-5 spinules. The maxilliped (Fig. 15) is 3-segmented. There are 2 naked setae on the second segment. The terminal segment bears proximally a spine with unilateral spinules, a hyaline naked setule, and near the base of the latter a minute setule; the segment is produced to form an attenuated spinelike structure with a row of long spinules along one side and a row of minute spinules near the opposite margin.

The postoral area (Fig. 16) shows between the paragnaths a shield-shaped area which projects ventrally to form a low median process. Posterior to the sclerotization which almost joins the

bases of the maxillipeds, the ventral surface of the cephalosome protrudes slightly (best seen in a lateral view, as in Fig. 2).

Legs 1-4 (Figs. 17, 18, 19, and 20) have trimerous rami except for the endopod of leg 4 which is unimerous. The armature of the legs is as follows (the Roman numerals indicating spines, the Arabic numerals setae):

P 1	protopod	0-1;	1-0	exp	I-0;	I-1;	III,I,4
				end	0-1;	0-1;	I,2,3
P 2	protopod	0-1;	1-0	exp	I-0;	I-1;	III,I,5
				end	0-1;	0-2;	I,II,3
P 3	protopod	0-1;	1-0	exp	I-0;	I-1;	III,I,5
				end	0-1;	0-2;	I,II,2
P 4	protopod	0-1;	1-0	exp	I-0;	I-1;	II,I,5
				end	II		

The inner seta on the coxa of legs 1-3 is long and plumose, but in leg 4 this seta is minute (7 μ long) and naked. In the first 3 legs the inner margin of the basis bears a short row of hairs, but in leg 4 these hairs are lacking. The outer coxal margin of leg 1 is expanded to form a prominent lobe (Fig. 17); in legs 2 and 3 this expansion is much less prominent and in leg 4 it is apparently absent. The tips of the outer spines on the exopods are slightly recurved posteriorly and the more proximal ones have minute terminal flagella. The 3 spines on the last segment of the endopod of leg 2 are 14, 10, and 13 μ in length from proximal to distal, with the middle one having a short terminal flagellum. In leg 4 the exopod is longer than in any of the preceding legs. The endopod measures 53 x 16 μ and has nearly parallel margins without a constriction or notch. It bears a row of hairs on its outer proximal third and an anterior row of small spinules near the insertions of the 2 divergent terminal spines (the outer 18 μ long with a minute flagellum, the inner 37 μ long with a more strongly spinulose flange along the outer side than along the inner side).

Leg 5 (Fig. 21) consists of a strong spine (33 μ long) and an adjacent seta (21 μ), together with a dorsal seta (22 μ), ornamented as in the figure. External to the spine and seta there is a row of minute blunt spinules at the apex of the segment. Although, as in other species of *Pseudanthessius*, there is no free segment of leg 5, it is likely that the spine and its adjacent seta correspond to the terminal armature in other lichomolgids.

Leg 6 is probably represented by the 2 setae near the attachment of each egg sac (see Fig. 4).

The color in life in transmitted light is translucid, the eye red, the intestine black, the ovary gray, the egg sacs opaque gray. (Although in specimens preserved in 70 per cent ethyl alcohol the color is an opaque grayish brown, the color changes quickly to a bright red when the copepods are placed in lactic acid.)

Male. — The body (Figs. 22 and 23) has a much narrower prosome than in the female, but otherwise resembles that sex in general form. The length (not including the setae on the caudal rami) is 0.76 mm (0.73-0.78 mm) and the greatest width is 0.27 mm (0.25-0.28 mm), based on 10 specimens (including the allotype, 8 paratypes, and 1 specimen from Pte. Ambarionaomby on October 30). The ratio of length to width of the prosome is 1.57 :1.

The segment of leg 5 is similar to that of the female, and measures 31 x 94 μ. The genital segment (Fig. 24) is nearly as long as wide, 104 x 110 μ, and in dorsal view has a subspherical outline. In lateral view (Fig. 25) the anteroventral part of the segment projects noticeably. There is no intersegmental sclerite between the segment of leg 5 and the genital segment. The 4 postgenital segments are 39 x 52, 32 x 51, 30 x 50, and 43 x 53 μ from anterior to posterior.

The caudal ramus resembles that of the female, but is a little shorter, the inner length being 78 μ, the outer length 73 μ, the width 23 μ, and the ratio of length to width 3.26 :1.

The surfaces of the prosome and urosome bear minute setules as in the female. The ratio of the length of the prosome to that of the urosome is 1.31 :1.

The rostral area, first antenna, second antenna, labrum, mandible, paragnath, and first maxilla are like those in the female. The second maxilla also resembles that of the female, but lacks the small sclerotized protuberance on the expanded margin of the basal segment. The maxilliped (Fig. 26) is much elongated, slender, and 4-segmented (assuming that the fourth segment is represented by the proximal part of the claw). Its entire length including the claw is about 300 μ. The first segment is unarmed. The second bears 2 unequal inner setae and 2 rows of hairs, one along the inner margin distal to the setae and another starting on the proximal inner margin and passing obliquely to the distal posterior surface of the segment. The very short third segment is unarmed. The terminal recurved claw, 135 μ in length along its axis, bears a conspicuous terminal lamella. The slightly crenated fringe along its concave margin is interrupted about midway. Near the base of the claw on its posterior surface there is a seta

42 μ long with minute lateral spinules, and on its anterior surface there are 2 small naked setules, one 10 μ, the other 4 μ long.

The postoral area is like that of the female.

Legs 1-4 resemble those of the female except that the last segment of the endopod of leg 1 is more elongated (Fig. 27), and the terminal segment of the endopod of leg 2 is more elongated, and its 3 spines are longer (24, 22, and 25 μ from proximal to distal), as seen in Figure 28.

Leg 5 is similar to that of the female.

Leg 6 (Fig. 29) consists of a posteroventral flap on the genital segment. Beyond the rim of the segment the leg projects conspicuously (see Fig. 24) as a large, pointed, ventral sclerotized process dorsal to which there is a shorter rounded process bearing 2 naked setae 22 and 24 μ in length.

The spermatophore, seen only inside the body of the male (Fig. 24), is oval, about 72 x 45 μ, with a short neck.

The color in life in transmitted light resembles that of the female.

RELATIONSHIP TO OTHER SPECIES IN THE GENUS

Twelve species of *Pseudanthessius* may be readily distinguished from *P. procurrens* in that they lack the prominent outer expansion on the coxa of leg 1 and do not bear the two rounded sclerotized lobes on the anterior part of the genital segment in the female. These species are: *P. aestheticus* Stock, Humes, and Gooding, 1963, *P. concinnus* Thompson and A. Scott, 1903, *P. deficiens* Stock, Humes, and Gooding, 1963, *P. dubius* G. O. Sars, 1918, *P. graciloides* Sewell, 1949, *P. luculentus* Humes and Cressey, 1961, *P. mucronatus* Gurney, 1927, *P. nemertophilus* Gallien, 1935, *P. notabilis* Humes and Cressey, 1961, *P. pectinifer* Stock, Humes, and Gooding, 1963, *P. tortuosus* Stock, Humes, and Gooding, 1963, and a new species (Humes and Ho, in press) from a polychaete annelid in Madagascar.

Eight other species may be separated from *P. procurrens* in that they lack the two lobes on the anterior part of the genital segment in the female and have a different armature on the last segment of the second antenna. (Unfortunately, in the original descriptions of these species, definite information on the condition of the outer coxal margin of leg 1 was not given.) These species are: *P. gracilis* Claus, 1889, *P. latus* Illg, 1950, *P. obscurus* A. Scott, 1909, *P. sauvagei* Canu, 1892, *P. spinifer* Lindberg 1945, *P. tenuis* Nicholls, 1944, *P. thorelli* (Brady, 1880), and *P. weberi* A. Scott, 1909.

Three species remain to be compared with *P. procurrens*: *P. liber* sensu Sewell, 1949, *P. liber* (Brady, 1880), and *P. assimilis* G. O. Sars, 1917. The species referred to as *P. liber* (Brady and Robertson) by Sewell (1949) is probably a new and unnamed species of the genus (see Humes and Cressey, 1961, pp. 80-81). It differs from *P. procurrens* chiefly in the presence of two long elements (aesthetes ?) on the basal segment of the first antenna, in the inwardly curving terminal spine on the last segment of the exopod of legs 2-4, and in the notch on the outer margin of the endopod of leg 4. No information was given for this form regarding the nature of the genital segment in the female, and the condition of the outer coxal margin of leg 1 is not clearly shown in Sewell's text figure 32 D.

P. liber (Brady, 1880)[2] lacks the two lobes on the anterior part of the genital segment of the female, has a caudal ramus about twice as long as wide, and has a different armature on the last segment of the second antenna. Brady did not mention an outer coxal expansion on leg 1, but Sars (1917) both mentioned and figured such an expansion in specimens taken in Norway. The expansion illustrated on Sars' plate XCIV is, however, less pronounced than in *P. procurrens*. The armature for the last segment of the endopod of leg 3 in the female is, according to Sars, I,II,3, instead of I,II,2 as in the Madagascan species.

P. assimilis G. O. Sars, 1917, is said by Sars to be closely allied to *P. liber* (Brady, 1880). Like the latter species it lacks the two lobes on the genital segment of the female and has an armature on the last segment of the second antenna unlike that of *P. procurrens*. Sars stated that the legs are "almost exactly as in *P. liber*," implying that there is a similar outer coxal expansion on leg 1.

Judging from the available information, *P. procurrens* appears to be near both *P. liber* (Brady, 1880) and *P. assimilis* G. O. Sars, 1917, resembling them in having an outer coxal expansion on leg 1, but differing in having two lobes on the anterior part of the genital segment in the female and in having a different armature on the last segment of the second antenna.

SUMMARY

The new species *Pseudanthessius procurrens* is associated with the cidarid echinoid *Phyllacanthus imperialis* (Lamarck) in the

[2] Not Brady and Robertson, 1876. See Stock, Humes, and Gooding, 1963, p. 10, footnote.

region of Nosy Bé, northwestern Madagascar. Within the genus the copepod may be recognized by the conspicuous expansion on the outer coxal area of leg 1 and by the two rounded lateral lobes on the anterior part of the genital segment in the female. The species nearest to the new form appear to be *P. liber* (Brady, 1880) and *P. assimilis* G. O. Sars, 1917. Although the host echinoderm is widely distributed in the Indo-Pacific area, the new copepod associated with it is known at present only from the type locality in Madagascar.

REFERENCES CITED

Brady, G. S.

1880. A monograph of the free and semi-parasitic Copepoda of the British Islands. Ray Society, London, **3**:1-83.

Brady, G. S. and D. Robertson

1876. Report on dredging off the coast of Durham and North Yorkshire in 1874. Rept. British Ass. Adv. Sci. (Bristol), **45**: 185-199.

Canu, E.

1892. Les Copépodes du Boulonnais, morphologie, embryologie, taxonomie. Trav. Lab. Zool. mar. Wimereux-Ambleteuse (Pas-de-Calais), **6**:1-354.

Claus, C.

1889. Über neue oder wenig bekannte halbparasitische Copepoden, insbesondere der Lichomolgiden- und Ascomyzontiden-Gruppe. Arb. Zool. Inst. Univ. Wien, **8**(3):327-370.

Gallien, L.

1935. *Pseudanthessius nemertophilus* nov. sp., copépode commensal de *Lineus longissimus* Sowerby. Bull. Soc. Zool. France, **60**:451-459.

Gurney, R.

1927. Zoological results of the Cambridge expedition to the Suez Canal, 1924, XXXIII. Report on the Crustacea: — Copepoda (littoral and semi-parasitic). Trans. Zool. Soc. London, **22**(4):451-477.

Humes, A. G. and R. F. Cressey

1961. Deux nouvelles espèces de *Pseudanthessius* (Copepoda, Cyclopoida) parasites des oursins à Madagascar. Mém. Inst. Sci. Madagascar, sér. F, 1959, **3**:67-82.

Humes, A. G. and J.-S. Ho

In press. New cyclopoid copepods associated with polychaete annelids in Madagascar. Bull. Mus. Comp. Zool.

Illg, P.

1950. A new copepod, *Pseudanthessius latus* (Cyclopoida: Lichomolgidae) commensal with a marine flatworm. Jour. Washington Acad. Sci., **40**(4):129-133.

Lindberg, K.

1945. Un nouveau copépode poecilostome de l'Inde de la famille des Lichomolgidae; *Pseudanthessius spinifer*, n. sp. Bull. Soc. Zool. France, **70**:81-84.

Nicholls, A. G.

1944. Littoral copepods from South Australia (II). Calanoida, Cyclopoida, Notodelphyoida, Monstrilloida and Caligoida. Rec. So. Austr. Mus., **8**(1):1-62.

Sars, G. O.

1917. An account of the Crustacea of Norway with short descriptions and figures of all the species. Vol. 6, Copepoda, Cyclopoida, pts. 11 and 12, Clausidiidae, Lichomolgidae (part), pp. 141-172. Bergen Museum, Bergen.

1918. An account of the Crustacea of Norway with short descriptions and figures of all the species. Vol. 6, Copepoda, Cyclopoida, pts. 13 and 14, Lichomolgidae (concluded), Oncaeidae, Coryeaeidae, Ergasilidae, Clausiidae, Eunicicolidae, Supplement, pp. 173-225. Bergen Museum, Bergen.

Scott, A.

1909. The Copepoda of the Siboga Expedition. Part I. Free-swimming, littoral and semi-parasitic Copepoda. Siboga Exped., **29**a:1-323.

Sewell, R. B. S.

1949. The littoral and semi-parasitic Cyclopoida, the Monstrilloida and Notodelphyoida. John Murray Exped. 1933-34, Sci. Repts., **9**(2):17-199.

Stock, J. H., A. G. Humes, and R. U. Gooding

1963. Copepoda associated with West Indian invertebrates IV. The genera *Octopicola*, *Pseudanthessius* and *Meomicola* (Cyclopoida, Lichomolgidae). Studies Fauna Curaçao and other Caribbean Is., **18**(77):1-74.

Thompson, I. C. and A. Scott

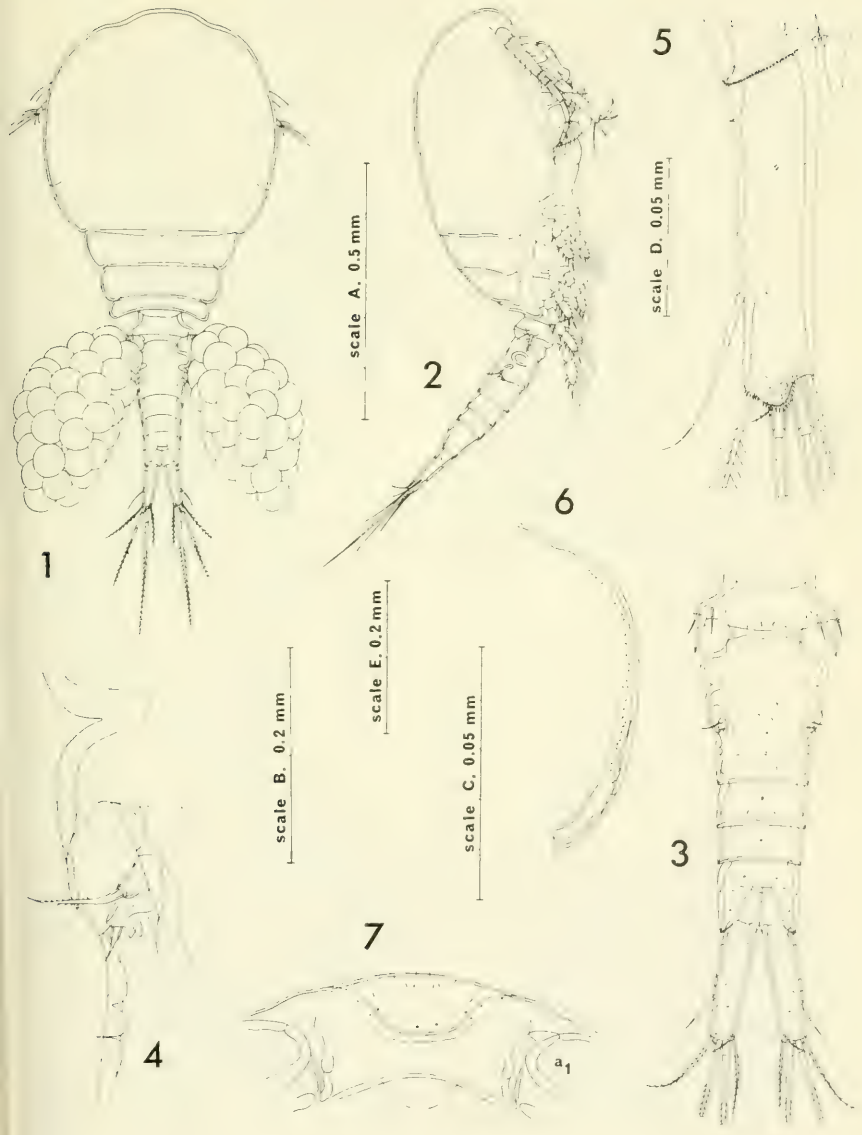
1903. Report on the Copepoda collected by Professor Herdman at Ceylon in 1902. Rept. Govt. Ceylon Pearl Oyster Fish. Gulf of Manaar, pt. I, Suppl. Rept. No. 7:227-307.

(Received December 10, 1965.)

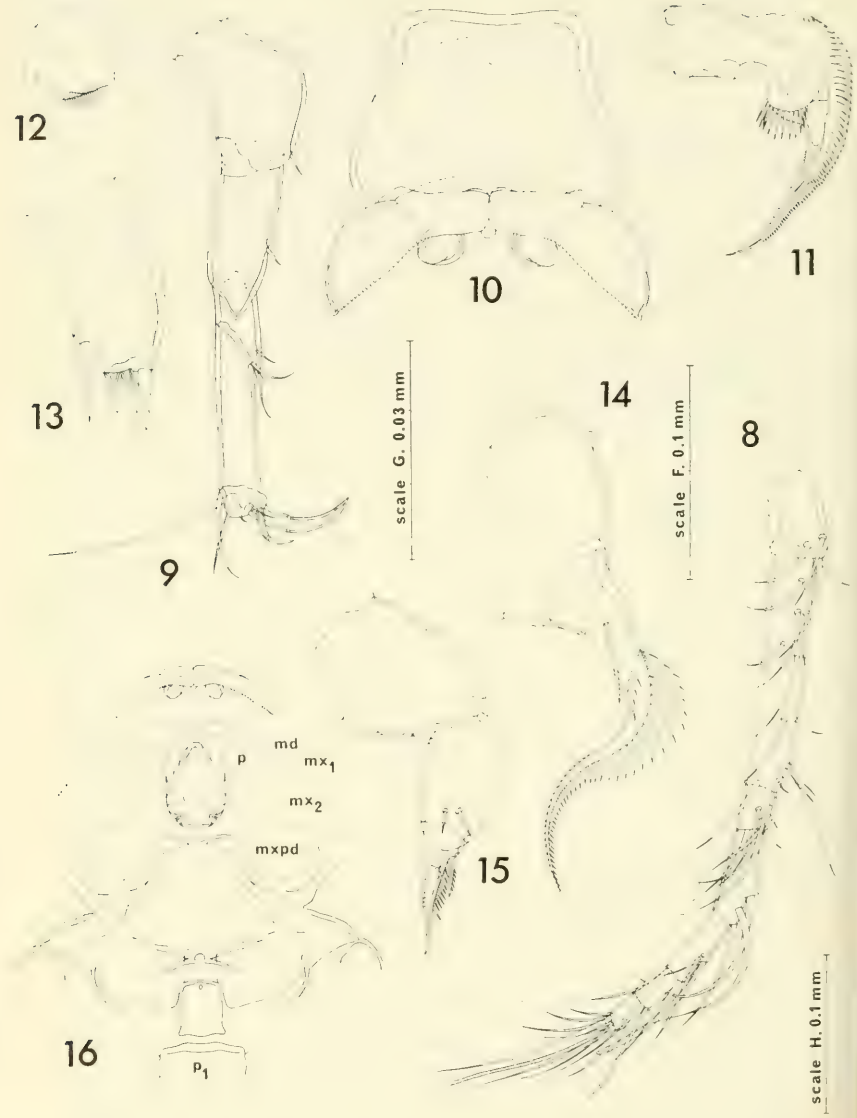
EXPLANATION OF THE FIGURES

All the figures have been drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which the figure was drawn.

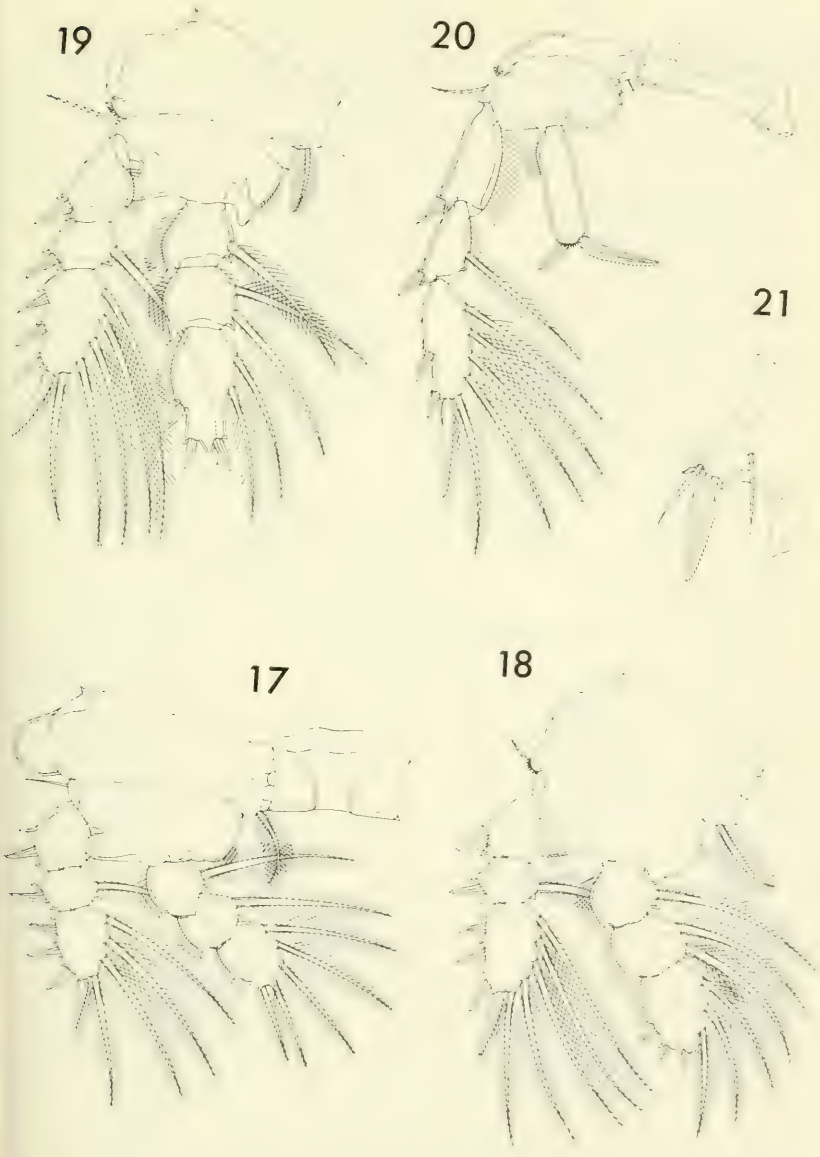
Abbreviations: a_1 = first antenna, md = mandible, p = paragnath, mx_1 = first maxilla, mx_2 = second maxilla, mxpd = maxilliped, p_1 = leg 1.



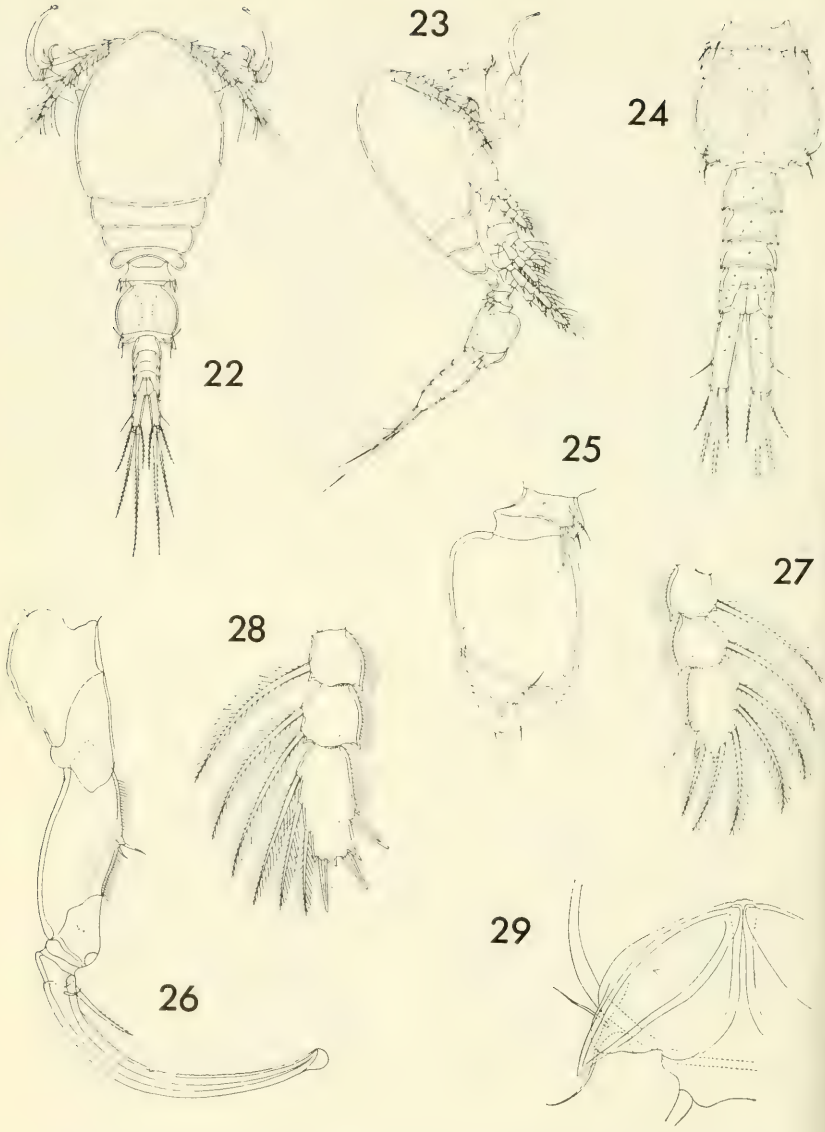
FIGURES 1-7. *Pseudanthessius procurrens* n.sp., female. 1, dorsal (A); 2, lateral (A); 3, urosome, dorsal (B); 4, area of attachment of egg sac, dorsal (C); 5, caudal ramus, ventral (D); 6, edge of cephalosome, ventral (E); 7, rostral area, ventral (F).



FIGURES 8-16. *Pseudanthessius procurrens* n.sp., female (continued). 8, first antenna, anterodorsal (F); 9, second antenna, inner (F); 10, labrum, ventral (D); 11, mandible, inner (D); 12, paragnath, ventral (D); 13, first maxilla, outer (G); 14, second maxilla, dorsal (D); 15, maxilliped, inner (D); 16, postoral area, ventral (H).



FIGURES 17-21. *Pseudanthessius procurrens* n.sp., female (continued). 17, leg 1, anterior (F); 18, leg 2, anterior (F); 19, leg 3, posterior (F); 20, leg 4, anterior (F); 21, leg 5, dorsal (D).



FIGURES 22-29. *Pseudanthessius procurrens* n.sp., male. 22, dorsal (A); 23, lateral (A); 24, urosome, dorsal (B); 25, genital segment, lateral (H); 26, maxilliped, anterior (F); 27, endopod of leg 1, anterior (F); 28, endopod of leg 2, anterior (F); 29, leg 6, ventral (D).

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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA

I. INTRODUCTION

BY ALFRED SHERWOOD ROMER

THE 1964-65 LA PLATA-HARVARD EXPEDITION

This is the first of a proposed series of papers giving the scientific results of a fossil-collecting expedition to western Argentina made during the summer of 1964-65 under the joint auspices of the Universidad de La Plata and Harvard University. The project grew out of the realization, during an earlier expedition of this sort, that further work in this area might result in important additions to the early tetrapod fauna of South America.

In 1958 a group of Harvard paleontologists under the direction of Prof. Bryan Patterson and myself, in cooperation with the Museo Argentina de Ciencias Naturales "Bernardino Rivadavia" de Buenos Aires, spent some months in exploring for vertebrate fossils in western Argentina. In part, Tertiary mammals were collected, and in part, fishes and brachyopid labyrinthodonts from the Triassic Cacheuta series of Mendoza Province (cf. Rusconi, 1951, etc., and Romer, 1960). Most especially, however, we explored and developed the Triassic beds of the Ischigualasto region in northeastern San Juan Province (cf. Romer, 1962); these proved exceedingly productive. Work on them has been continued by the Instituto Lillo of Tucumán, at first under Dr. Osvaldo Reig, currently under Sr. José F. Bonaparte.

The Harvard members of the 1958 party included, in addition to Prof. Patterson and myself, Arnold D. Lewis, chief preparator of the Museum of Comparative Zoology, James A. Jensen, then of the Harvard staff but now in charge of geological and paleontological collections at Brigham Young University (Provo, Utah), and Mrs. Ruth H. Romer. Prof. Patterson's interests have now shifted to another field. The others of the group, however,

became deeply interested in the problems of the early history of tetrapod life in South America, and felt that, if the opportunity should be presented, a second trip of exploration in western Argentina might quite possibly result in a major addition to this story.

Such an opportunity arose in 1964 through a grant from the National Science Foundation, from which could be met most of the costs of a field trip of the sort proposed. Accordingly, an agreement to this end was drawn up between the Harvard Museum of Comparative Zoology and the Museo de Universidad Nacional de La Plata. Under Argentinian law 9080 of 1911, all fossils are declared the property of the national government, under the Ministry of Education. A commission of three directors of leading museums is empowered by the Ministry to regulate the collection and disposition of fossil materials. Our agreement with the Museo de La Plata was approved by this commission. As provided by law, type specimens and other representative materials, or casts thereof, are to be deposited in the Museo de La Plata; other specimens remain the property of the Harvard Museum. Further, we are to be allowed to have for two years exclusive right to the study and description of specimens from any new fossil deposits discovered during the course of the work.

Our objective was to find fossil localities for reptiles and amphibians in horizons in the Permian or in Triassic beds earlier than that of Ischigualasto. Although the position of the Ischigualasto fauna is somewhat debatable, it is essentially middle Triassic in character, predominantly one of rhynchosaurs and cynodonts of gomphodont type; there are known a few advanced thecodonts, but only the bare beginnings of the dinosaur fauna which dominates the scene in the late Triassic. Faunas comparable to that of Ischigualasto are known in Brasil (Santa María) and in Africa (Manda beds); but while antecedent Permian and Lower Triassic faunas are abundant in Africa, almost nothing was known of earlier tetrapods in South America. On that continent no tetrapod has ever been reported from the Permian of Argentina, and elsewhere nothing is known except for the aberrant aquatic *Mesosaurus* of southern Brasil (and South Africa) and a single labyrinthodont from the Brasilian Permian (Price, 1948). The earlier Triassic was, before our recent exploration, almost equally unknown as regards reptilian faunas. It is possible that, despite general beliefs as to its late Triassic position, the Cacheuta series may be of early Triassic age (cf. Reig, 1961), but the evidence is far from conclusive, and

little reptilian material is known from this series. Recently, two forms, a dicynodont and a gomphodont, were discovered in southern Mendoza Province and are now being studied by Sr. Bonaparte; these are probably early Triassic in age.

This short list is a complete roster of all tetrapod vertebrates known from any part of South America in deposits older than the relatively late Triassic of the Ischigualasto Formation and the essentially comparable Santa María beds of Brasil. A great deal of stratigraphic work has been done in western Argentina by the geologists of the Instituto Nacional de Geología y Minería, the Yacimientos Petrolíferos Fiscales and the Comisión Nacional de Energía Atómica, and some thousands of square miles of continental deposits have been mapped as presumably Permian or Triassic in age. But apart from a few finds of fishes, not a single vertebrate fossil was discovered in any of these seemingly barren beds. It was thus not impossible that our trip might have been a complete failure, and that the entire four months planned for field work might have ended without our finding a single specimen.

Geologists, however, intent on stratigraphic work, are notoriously liable to overlook fossil materials for which the eye of the paleontologist is trained. Our obvious plan of campaign was to visit, one after another, "sample" areas in which Permian or Triassic rocks had been mapped, and to hope that, ultimately, one or more of these widespread regions might yield a worthwhile fauna. We found the geologists of the various Argentinian services mentioned exceedingly generous and helpful in giving us their advice and free access to unpublished maps, manuscripts, and field notes to aid in our laying out a plan of campaign and in discussing matters of stratigraphy and faunal succession. We wish to thank these friends for their help. They include, amongst others: Director General Félix González Bonorino, Dr. Roberto V. Tezón, Vocal del Directorio del Instituto, Dr. Juan C. Turner, Dr. Eduardo Holmberg, Dr. Francisco Fidalgo, Dr. Guillermo Furque, Dr. Emilio González Díaz, and Sr. Carlos Turcogreco, of the staff of the Instituto Nacional de Geología y Minería; Dr. Eduardo Rolleri, Dr. Miguel Flores, Dr. Alberto Mingramm, Dr. Pedro Criado Roque, Dr. Héctor F. de la Mota, of the Yacimientos Petrolíferos Fiscales; Profs. Sergio Archangelsky, Angel V. Borrello, and Alfredo Cuerda, of the Universidad de La Plata; Prof. Arturo Amos of the Universidad de Buenos Aires; Dr. Pedro N. Stipanicic, director of geological work for the Comisión

Nacional de Energía Atómica; and Sr. José F. Bonaparte of the Instituto Miguel Lillo de Tucumán.

The major part of the funds which made the expedition possible was furnished by grant GB-2454 of the National Science Foundation. The cost of the motor vehicles and a fraction of the travel expense were supplied from private sources. We wish to thank Brigham Young University for allowing Mr. Jensen to accompany us, and the Museum of Comparative Zoology for making it possible for Mr. Lewis to take part. Publication of this paper was aided by NSF grant GB-4615.

Our collaboration with the Museo de La Plata proved exceedingly advantageous. Professor Rosendo Pascual aided us in every way before, during, and after our months in the field, and for a large fraction of the time was an active member of the field party. We are very grateful to Dr. and Señora Pascual for their hospitality in La Plata before and at the close of the field season. Dr. Mario Teruggi, Dean of Natural Sciences and Director of the La Plata Museum, aided greatly in solving our difficulties with the provincial government. Very welcome was the hospitality given us by the University at Samay Huasi, "the house of repose." This had been the country estate of Dr. Joaquín B. González, famous Argentinian author, statesman, and educator, and is located near the city of Chilecito in La Rioja Province. Willed by him to the University at his death, it is now used as a resort for artists, writers, and faculty members. An irrigated desert oasis of some 40 acres or so, with splendid groves of trees, vineyards, and gardens, it contains a spacious and well-equipped house, with a permanent staff. Most of our work proved to lie in La Rioja Province; Chilecito was the best available town to visit periodically for supplies, and we greatly enjoyed on these occasions the amenities afforded by Samay Huasi through Sr. and Sra. Amoretti and their staff, and Prof. Bongiorno of the University who has charge, in addition to other duties, of a museum at Samay Huasi.

Our equipment for the trip was carefully selected by Mr. Lewis, on the basis of his experience on the previous expedition, to the end of attempting to make our work under the somewhat trying conditions of summer in the arid regions of western Argentina as efficient and as comfortable as possible. For rolling stock we took with us a 4-wheel-drive Jeep and a ½ ton stake-bodied truck, likewise with 4-wheel traction, and equipped with a 75-gallon water tank and spare gasoline tanks. Most useful, as it proved, was a "tote-gote" — a motorcyclette of a type recently

developed in the western United States for traversing rough country and steep grades, and able to carry a modest load of materials in addition to the rider. Without this, our work would have been severely handicapped, for part of our best collecting areas proved to be one or two miles from the closest point we could reach with a jeep; the laborious business of attempting to carry in on our backs many hundreds of pounds of plaster and hundreds of gallons of water, and return with some thousands of pounds of plaster blocks, would have greatly reduced our results.

Our party arrived in Argentina the latter part of October, and set out for the field after a short stay in La Plata and Buenos Aires to complete our equipment and obtain all possible data and advice. We then began our planned series of visits to typical areas of sediments mapped as presumed Permian or Triassic in western Argentina. As the discussion above would suggest, our expectations of success at any given locality were none too sanguine, and for the first two months of the trip our gloomiest forebodings appeared to be realized; during this time we failed to find the slightest scrap of tetrapod bone in any new area.

The Santa Clara Formation occupies a considerable area in the precordillera between Mendoza and San Juan. It has sometimes been thought to be Triassic in age, but is believed by Dr. H. J. Harrington (1941, 1956) to be Permian. A few fishes (Bordas, 1944) and a single footprint (Rusconi, 1951a, 1956, and Peabody, 1955) had been described from the Santa Clara, but no tetrapod fossils. We first camped near the puesto of Santa Clara, near the north end of the area covered by the formation, at the east margin of the precordillera in southern San Juan Province, and explored this area. Here the Santa Clara shales and sandstones, some thousands of feet thick, form a series of mountains separated by deep valleys. We found further remains of fishes in the area of original discovery, and a further fish locality in shales north of the Quebrada de la Montaña a short distance east of the boundary between the Santa Clara beds and the Villavicencio group. In addition, a series of trackways of rather poor quality was found and cast; these were situated a short distance up a senda leading south from the Quebrada de la Montaña to Puesto Alojamiento. But as far as our sampling of these vast exposures went, they appeared to be entirely barren of tetrapod osseous remains.

A second camp was made in the southern area of the Santa Clara Formation, in the canyon of the Río de las Peñas, between

Cerro Peña and Cerro Palado de las Higueras. Footprints had been previously reported from this area. We learned later that Sr. Bonaparte had made a visit to this area previous to ours. Like him, we found the region to be exceedingly rich in reptilian trackways, in a fashion comparable to areas of the famous Connecticut Valley Triassic. The trackways, however, are in the main obviously those of dinosaurs or advanced thecodonts, and the beds are presumably middle or late Triassic in age, despite the presence of "*Chirotherium*"-like footprints. As in the northern part of the Santa Clara Formation, we failed to find any bones; not even fish specimens were discoverable.

Bodenbender (1911, etc.) had described at length as "Paganzo II" a very thick series of red sandstones, presumably Permian in age, from La Rioja Province. These are present in the region of the Sierra de Sañogasta, its southern continuation, the Sierra de Vilgo, and the country south of the mountains, between the village of Paganzo and the railway junction of Patquia to the east. We spent many weary days walking these sandstones from the region of Patquia northward towards Chilecito, and in the region of Los Colorados railway station. We found not the slightest trace of animal life in these abundant exposures of "Paganzo II"; not a bone, not even a fish scale or a footprint. Following this discouraging period, we took time out for a brief visit to Tucumán, where we were hospitably received at the Instituto Lillo by Director Willink, and profited by discussion with Sr. Bonaparte.

Permo-Triassic beds had been studied in the Sierra de las Quijadas in northwestern San Luis Province by Sr. José Román Guinazú of San Luis, and footprints from this region were described by Lull (1942). The group spent some time there. The best exposures lay in a deep amphitheatre, difficult of access, west of Puesto Hualtarán. From the nearest approach by car there was necessary a long, tortuous walk, followed by a horse-trail descent of several hundred meters into the base of the amphitheatre; the return at the end of a day involved the wearisome ascent of the canyon walls. Here, as in other areas previously explored, not a bone was found, although a number of footprints of middle to late Triassic type were seen in the deepest and lowest beds of the area.

Permian sediments had been reported in the Sierra de los Llanos of southern La Rioja (Bracaccini, 1946). Here we found massive red conglomerates and grey plant-bearing shales. Neither type of sediment appeared promising as a possible source of

tetrapod remains, and only a very short time was spent in this area.

Having thus prospected for the better part of two months in some five areas with completely negative results, we had become somewhat disheartened. As some slight alleviation, we decided to visit for a short time our old "stamping ground" of Ischigualasto, for the purpose of collecting fresh material of rhynchosaurs, which by agreement with Sr. Bonaparte, I am studying. We had, in our discouragement, half come to believe that perhaps we had lost the ability to see fossil bones even if present. Ischigualasto disabused us of that apprehension; a good selection of rhynchosaur specimens was obtained.

The Christmas season had now arrived, and we stopped work to spend a few days at Samay Huasi. But despite the beauty and amenities of that place, the holidays were far from joyful for us. Half of our field time had been consumed, and we had thus far met only with utter failure.

But a complete reversal of fortune now occurred. Among the places remaining for possible investigation, one which appeared particularly attractive was an area in western La Rioja Province, west and south of Chilecito, west of the Sierra de Sañogasta, and about three hours distant from Chilecito by car. Here, at the east margin of the barren Campo de Talampaya, along the rivers Talampaya, Chañares, and Gualo, geological reconnaissance by Bodenbender (1911, etc.) and, in recent years, by de la Mota and Fidalgo (unpublished) had shown the presence of a varied series of sediments of Permian and Triassic age. No fossils had been seen, but in view of the considerable range in time occupied, and the probability of a variety of sediments in the succession of formations which appeared to be present, one might not unreasonably hope that vertebrates might somewhere be found.

This hope was abundantly justified. We first pitched camp in the southern part of the area, near the elevation known as the Mogote del Gualo and near the only spring of any importance in this arid region. On our first day of prospecting, fragmentary vertebrate remains were discovered; the next day several good specimens of dicynodonts came to light; from that day on until we stopped work some seven weeks later, not a day passed without the discovery of worthwhile reptilian material. From our first camp we presently moved some miles to the northwest to camp near the point where the Río Gualo emerges from the hills into the flat Campo de Talampaya. Finding that still richer fossil deposits were present farther to the north, in the valley of the Río

Chañares, we camped for the remainder of our stay on the banks of that stream.

In the following article in this series there will be given a resumé of the geology of the area. The region is only a short distance from the Ischigualasto Valley on the opposite, western, side of the Campo de Talampaya, and several of the later Triassic formations in the Chañares-Gualo region could be readily identified with the Los Colorados, Ischigualasto, and Los Rastros formations with which we had become familiar on our earlier trip. No fossils were found by us in the limited exposures of the first two; in the carbon-bearing Los Rastros a small amount of fish material was seen, and more could probably have been collected had we not found other, more profitable work. In rather lower beds, perhaps of Permian age, which we are terming the Tarjados Formation, fragmentary reptile remains were found in two areas, and not improbably intensive work would result in further finds. Nearly all our finds, however, were derived from a series of volcanic tuffs underlying the Los Rastros beds, which we are terming the Chañares Formation. These include some 75 meters of distinctive blue-white beds, easily traceable across the region despite the presence of numerous faults. Almost all the fossil remains, we presently discovered, occurred in the lowest 10 meters or so of these beds, and in most areas a careful following of the base of the Chañares resulted in the discovery of fossil specimens at frequent intervals. Some of the specimens were found simply buried in the tuffs. In a large proportion of cases, however, they were enclosed in grey-brown colored nodules of coarser tuffs. A fraction of such nodules proved to be barren; in some areas, however, almost every nodule would contain a skull or skeleton, and in some cases, two or three individuals would be represented in a single nodule. Never had any of us encountered a fossil-collecting area of equal richness. To add to our pleasure, it was obvious in the field that preparation of the specimens (unlike much of the material collected at Ischigualasto on our earlier expedition) could be readily accomplished.

Apart from a large dicynodont, almost all the specimens were forms of small size; the skulls averaged but a few inches in length. More than 150 good skulls were collected and, in addition, large amounts of posteranial materials. At the time this is written, little of the material has been prepared, but apart from

a relatively small fraction of "problematica," the general systematic position of most of the specimens was evident when collected. There appears to be but a single type of dicynodont, apparently of the general *Kannemeyeria* type. A considerable fraction of the finds were those of small thecodonts, some, at least, appearing to be forms on the pattern of *Euparkeria* of the *Cynognathus* zone of South Africa (recently redescribed by Ewer, 1965). The greater part of the collection, however, consists of small cynodonts; part of them are carnivorous, but the greater number are "gomphodonts," in which the cheek teeth form a grinding battery.

THE TRIASSIC FAUNAL SEQUENCE

The position of the Chañares fauna in the Triassic sequence will, I trust, become apparent as its components are described in future numbers of this series. Meantime, a brief discussion of our current knowledge of the sequence of Triassic continental vertebrate faunas seems merited. The Triassic is commonly divided into Lower, Middle, and Upper portions stratigraphically — or in chronologic terms, early, middle, and late — in agreement with the three-fold division of the European Triassic (as indicated by the period name) into Bunter, Muschelkalk, and Keuper. On the basis of marine faunas, a series of stages — Scythian, Anisian, Ladinian, Carnian, Norian, and (as a transition to the Jurassic) Rhaetic — have been erected. It is frequently attempted to fit the vertebrate faunas into this sequence of stages. For the most part, however, this cannot be done with any degree of accuracy, because of the rarity of actual continuity of beds containing continental vertebrate faunas with marine strata which can be assigned a definite place in the stage sequence; most of the stage names are derived from Alpine beds far removed from continental areas. The only major exceptions have to do with the "Eotriassic" Scythian zone. As both Watson (1942) and Lehman and others (1959) have shown, the *Cynognathus* and *Lystrosaurus* zones of South Africa are definitely to be regarded as "Eotriassic" and Scythian in age[1] mainly on the basis of labyrinthodonts; the Moenkopi of the early North American Triassic and the Bunter of Europe are equally well assignable to the

[1] Huene (1956) has at times tabulated the *Cynognathus* zone as middle Triassic, but has cited no reason for this.

Scythian on the basis of their content of labyrinthodonts — labyrinthodonts of types not too far removed from those of the "Eotriassic" of Greenland and Madagascar. At present it is perhaps best to avoid commitment of specific faunas to specific marine stages in attempting to define a continental vertebrate sequence.

In the early years of this century our knowledge of a Triassic vertebrate sequence was very limited. For the early Triassic, we knew little of continental forms (apart from amphibians) except in the Upper Beaufort (*Lystrosaurus* and *Cynognathus* zones) of South Africa. Here, therapsids, most notably a variety of cynodonts, constituted the bulk of the fauna; archosaurs, in the form of primitive or aberrant thecodonts, were present in modest numbers; other reptiles were small in numbers and variety. At the other end of the Triassic sequence, a late reptilian assemblage of very different nature, consisting almost entirely of dinosaurs and advanced thecodonts, was known from a variety of redbeds formations, such as the Keuper of Europe, the Newark, Chinle, etc. of North America, and the redbeds of the Upper Stormberg of South Africa. Between, continental faunas of possible middle Triassic age were practically unknown, for the European Muschelkalk is marine, other middle Triassic beds of the northern continents are also marine, and the Molteno of South Africa had yielded no fossils except plants.

With the predominance of therapsids in the early Triassic, and of thecodonts and dinosaurs toward the end of the period, it was generally assumed that middle Triassic reptile faunas, if and when discovered, would exhibit a simple transition between these two extremes, with therapsids on the wane and with thecodonts advancing and showing the beginning of the dinosaur radiation. We are now in process, however, of gaining from Africa and South America a seemingly representative series of middle Triassic faunas — from the Santa María beds of Brasil, the Manda beds of East Africa and, most recently, the Ischigualasto beds of Argentina. To some degree these faunas show expected intermediate characters, for they contain advanced thecodonts and the beginnings of the dinosaurs. But the faunas show striking positive characters. Therapsids are rather restricted in variety, but show a surprising abundance of "gomphodont" cynodonts. Equally surprising and striking in these faunas is the overwhelming abundance of rhynchosaurs, almost unknown in earlier or later beds.

While it is premature, I think, to tie them down to specific marine stages, or to characterize them as "early," "middle" or "late" in any restrictive way, I believe it is clear that there are three successive stages in the faunal history of continental Triassic vertebrates:

(A) An early assemblage, of which the faunas of the *Lystrosaurus* and *Cynognathus* zones of South Africa, and the Wuhsiang beds of Shansi (China) are typical. There are abundant therapsids, principally cynodonts — mainly carnivorous, but with a few "gomphodonts" with molar-like cheek teeth. Thecodonts include generalized primitive forms such as *Euparkeria* and aberrant archaic types such as *Erythrosuchus* and *Chasmatosaurus*. Primitive rhynchosaurs are present but rare.

(B) The type of assemblage found in the Maleri, Santa María, and Ischigualasto beds. Carnivorous cynodonts persist, but are greatly overshadowed by abundant gomphodonts. Typical rhynchosaurs constitute a large fraction of the fauna. Thecodonts of advanced type are present, and a few early dinosaurs.

(C) The typical assemblages of the late Triassic, such as the Upper Keuper, South African redbeds, Lufeng series of Yunnan, Newark, Chinle, and Dockum of North America, and Los Colorados of Argentina. Therapsids are close to extinction. There are various advanced thecodonts, such as aetosaurids and (in the northern continents) phytosaurs, and numerous and varied dinosaurs, but rhynchosaurs are generally extinct.

One would, of course, expect assemblages transitional between these stages. It is probable, for example, that the Chañares fauna will prove to be intermediate between (A) and (B), and the same may be true of the Ntawere fauna of Zambia (Brink, 1963; Kitching, 1963). Of the faunas which we have listed under (B), that of Ischigualasto is perhaps relatively late, since several forms have already crossed the thecodont-saurischian boundary.

The typical (C) faunas are characterized in general by an abundance and variety of dinosaurs, the presence, in the Northern Hemisphere, of metoposaurs and phytosaurs, and the absence of rhynchosaurs and practical absence of therapsids. Certain beds usually placed in this category appear, however, either to be of earlier age than that of the typical (C) faunas, or else indicate regional late survival of certain of the forms characteristic of the (B) faunas. For example, the Maleri beds of India (Jain, Robinson, and Chowdhury, 1964) are generally assumed to be of relatively late Triassic age because of the presence of metoposaurs and phytosaurs. However, there is, in the restricted fauna

known, only one possible dinosaur, and rhynchosaurs persist. We may have here a (B)-(C) intermediate.

Baird and Take (1959) have recently discovered a reptilian fauna in the Wolfville sandstone of Nova Scotia, generally regarded as a basal member of the Upper Triassic Newark group. But quite in contrast with typical Newark faunas, Dr. Baird informs me that not only rhynchosaur remains, but a gomphodont, as well, are present. Quite surely we are here dealing with a fauna transitional between (B) and (C).

Rhynchosaurs are present in the Triassic fauna of the region of Elgin, Scotland, currently being restudied by Walker. Because of the close resemblance between *Stagonolepis* of Elgin and *Aetosaurus* of the German Keuper, Walker (1961) believes the Elgin fauna to be late Triassic in age. There is, however, no reason to believe that the aetosaurid type of thecodont was particularly short-lived; it was already present in the Ischigualasto fauna (Casamiquela, 1960). Possibly the Elgin fauna is transitional between (B) and (C); but the absence of dinosaur remains, except for *Ornithosuchus* (Walker, 1964) — a form so primitive that it has generally been regarded as a thecodont — strongly raises the question as to whether the Elgin fauna may not really belong in the (B) category and be of middle Triassic age. Rhynchosaurs are known from several English localities which are classified as "Keuper." But it will be noted that there is no English equivalent of the Muschelkalk of the continent; the early Triassic "Bunter" equivalents are immediately followed by redbeds of "Keuper" type, and it is quite possible that part or all of the English rhynchosaurs are of middle Triassic age.

In sum, it appears to be a reasonable working hypothesis that the Triassic included a sequence of three successive continental vertebrate faunas characterized by a dominance of (A) therapsids, (B) gomphodonts and rhynchosaurs, and (C) dinosaurs. We cannot, of course, expect completely clean-cut distinctions between the three; but a clear pattern seems to be emerging.

LITERATURE CITED

Baird, D., and W. F. Take

1959. Triassic reptiles from Nova Scotia. Bull. Geol. Soc. Amer., **70**: 1565-1566.

Bodenbender, G.

1911. Constitución geológica de la parte meridional de La Rioja y regiones limítrofes (República Argentina). Bol. Acad. Nac. Cienc. Córdoba, **19**: 1-220.

Bordas, A. F.
1944. Peces triásicos de la Quebrada de Santa Clara (Mendoza y San Juan). Physis, **19**: 453-460.
Bracaccini, O.
1946. Los estratos de Paganzo y sus niveles plantíferos en la Sierra de Los Llanos (Provincia de La Rioja). Rev. Soc. Geol. Argent., **1**: 19-61.
Brink, A. S.
1963. Two cynodonts from the Ntawere Formation in the Luangwa Valley of Northern Rhodesia. Palaeont. Afr., **8**: 77-96.
Casamiquela, R. M.
1960. Noticia preliminar sobre dos nuevos estagonolepoideos argentinos. Ameghiniana, **2**: 3-9.
Ewer, R. F.
1965. The anatomy of the thecodont reptile *Euparkeria capensis* Broom. Phil. Trans. Roy. Soc. London, B **248**: 379-435.
Harrington, H. J.
1941. Investigaciones geológicas en las Sierras de Villavicencio y Mal País, Provincia de Mendoza. Bol. Dirección Minas y Geología, Rep. Argent., **49**: 1-31.
1956. Argentina. *In:* Handbook of South American Geology. Mem. Geol. Soc. Amer., **65**: 131-186.
Huene, F.
1956. Paläontologie und Phylogenie der niederen Tetrapoden. Jena, 716 pp.
Jain, S. L., P. L. Robinson, and T. K. R. Chowdhury
1964. A new vertebrate fauna from the Triassic of the Deccan, India. Quart. Jour. Geol. Soc. London, **120**: 115-124.
Kitching, J. W.
1963. The fossil localities and mammal-like reptiles of the Upper Luangwa Valley, Northern Rhodesia. South Afr. Jour. Sci., **59**: 259-264.
Lehman, J.-P., C. Chateau, M. Laurain, and M. Nauche
1959. Paléontologie de Madagascar. XXVIII. Les poissons de la Sakamena moyenne. Ann. Paléont., **45**: 177-219.
Lull, R. S.
1942. Triassic footprints from Argentina. Amer. Jour. Sci., **240**: 421-425.
Peabody, F. E.
1955. Occurrence of *Chirotherium* in South America. Bull. Geol. Soc. Amer., **66**: 239-240.
Price, L. I.
1948. Um anfibio labirintodonte da formação Pedra de Fogo, Estado do Maranhao. Ministerio da Agricultura. Bol. Serv. Geol. Min. Brasil, **124**: 1-32.

Reig, O. A.

1961. Acerca de la posición sistemática de la familia Rauisuchidae y del género *Saurosuchus* (Reptilia, Thecodontia). Publ. Mus. Cienc. Nat. Mar del Plata, **1**: 73-114.

Romer, A. S.

1960. Vertebrate-bearing continental Triassic strata in Mendoza region, Argentina. Bull. Geol. Soc. Amer., **71**: 1279-1294.

1962. The fossiliferous Triassic deposits of Ischigualasto, Argentina. Breviora, Mus. Comp. Zool., No. **156**, 1-7.

Rusconi, C.

1951a. Laberintodontes triásicos y pérmicos de Mendoza. Rev. Mus. Hist. Nat. Mendoza, **5**: 33-158.

1951b. Rastros de patas de reptiles pérmicos de Mendoza. Rev. Soc. Hist. Geog. Cuyo, **3**: 1-14.

1956. Mares y organismos extinguidos de Mendoza. Rev. Mus. Hist. Nat. Mendoza, **9**: 2-88.

Walker, A. D.

1961. Triassic reptiles from the Elgin area; *Stagonolepis, Dasygnathus* and their allies. Phil. Trans. Roy. Soc. London, B **244**: 103-204.

1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. Phil. Trans. Roy. Soc. London, B **248**: 53-134.

Watson, D. M. S.

1942. On Permian and Triassic tetrapods. Geol. Mag., **79**: 81-116.

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A TRIASSIC AMMONITE FROM THE HINDUBAGH REGION, BALUCHISTAN, WEST PAKISTAN

BY BERNHARD KUMMEL

Ammonites are extremely rare in the thick development of Triassic strata between Quetta and Hindubagh in West Pakistan. Only five specimens, mostly very poorly preserved, have been reported to date. Because of their rarity the documentation of one additional specimen of rather good preservation is warranted.

The first record of Triassic ammonites from this region of Baluchistan was by Mojsisovics (1896, p. 611; 1899, p. 44) who described a single specimen, collected by C. L. Griesbach from a loose block, 7 miles south of Hindubagh. This specimen was described as *Didymites afghanicus* Mojsisovics (1896; 1899, pl. 20, fig. 9) and assigned a Norian age. Vredenburg (1904), on the basis of surveys carried out in the summer of 1901, contributed some regional, stratigraphic, and paleontological data on these Triassic formations. This author reported the presence of *Monotis* cf. *salinaria* in fair abundance at a few horizons and localities and illustrated one specimen. In addition, he illustrated an ammonite-*Halorites* sp. The specimen was not found in place but from local conditions Vredenburg concluded that it had not been transported very far. These specimens plus others collected by Vredenburg were submitted to C. Diener who published his results in 1906. In this small collection Diener (1906) was able to recognize the following forms:

Monotis salinaria Schlotheim
Halorites sp. ind. aff. *subcatenato* Mojsisovics
Celtites sp. ind. (group of ? *acuteplicati*)
Paratibetites sp. ind. ex aff. *tornquisti* Mojsisovics
Dittmarites or *Distichites* ? sp. ind.
Rhacophyllites vredenburgi Diener

The generally poor state of preservation of the specimens available to Diener is well reflected in the uncertainty in the identifications. Of these specimens only *Monotis salinaria* and *Halorites* sp. ind. aff. *subcatenato* were obtained from the spot where they probably weathered out. All the rest of the specimens were picked up amongst transported boulders from the beds of rivers within the Triassic outcrop area. On the basis of this scanty data, both Vredenburg and Diener concluded that the strata enclosing these fossils are of Norian age. Additional geological observations on the Triassic formations of the Quetta-Hindubagh area have been made by Gee (in Heron, 1939, p. 26-27), by Williams (1959), and by the Colombo Plan Project (1961), but in these reports there is little additional paleontological data.

I have had the opportunity to spend a few days in the region between Quetta and Hindubagh examining these Triassic formations but was not successful in finding any fossils. Mr. S. A. Bilgrami entrusted to the writer a specimen found in a stream bed near a mine of the Pakistan Chrome Ltd., two miles east of Gwal Railway Station. This specimen is fairly well preserved and can be assigned with confidence to *Arietoceltites arietitoides* Diener, a species first described from the *Tropites* limestone exposed at Kalapani, Byans, in the Himalayas. This new specimen thus provides an additional link in the correlation of these Triassic formations of Baluchistan with the much better documented Himalayan sequence. The *Tropites* limestone of Byans has yielded 168 species of invertebrates of which 155 are ammonites. The fauna as a whole shows very strong affinities to the Upper Triassic faunas of the Mediterranean region. All of the fossil species were collected from a three foot bed of limestone; of special interest is the mixture in this bed of typical Carnian and Norian ammonite species. Since *Arietoceltites arietitoides* was a unique species previously known only in Byans, and its presence in a mixed fauna at that, it does not help in refining the age determination of the Baluchistan Triassic formations. Diener's (1912, p. 150) final words on the age of these Triassic rocks were that they were Norian in age.

SYSTEMATIC DESCRIPTION

Family TROPICELTITIDAE Spath, 1951

Genus Arietoceltites Diener, 1916

Arietoceltites arietitoides (Diener)

Figures 1a, b

Tropiceltites arietitoides Diener, 1906, p. 156, pl. 3, fig. 12; Diener, 1912, p. 125; Diener, 1916, p. 101; Spath, 1951, p. 94; Kummel, *in* Arkell, 1957, p. L171, fig. 201, 4.

This species is represented by a single specimen of 56.5 mm in diameter, 13.1 mm for the height of the adoral whorl, 13.8 mm for the width, and 35 mm for the diameter of the umbilicus. In degree of involution and general proportion, this specimen is very much like the type specimen. There are slight differences in ornamentation: in the Baluchistan specimen the ribs are rusiradiate in the adoral 1.5 volutions, whereas in the Byans specimen the ribs are more radial. In both specimens the ribs turn strongly forward on approaching the marginal furrows aligning the median keel. I do not believe that these differences in ornamentation are of any taxonomic significance. The Byans material available to Diener (1906) consisted of the type specimen plus a few fragments. With this one additional specimen there is insufficient data available to evaluate the range of variability in these features. However, on the basis of experience with populations of comparable forms, one should expect a range of variability that would include that expressed by these two specimens. The suture was only partially exposed on Diener's type specimen and is not preserved in the specimen recorded here.

Occurrence. — From stream bed near mine of Pakistan Chrome Mines Ltd., two miles east of railway station at Gwal, presumably from Alozai group, between Quetta and Hindubagh, West Pakistan.

Repository. — Geological Survey of Pakistan, Quetta, West Pakistan.

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REFERENCES

ARKELL, W. J. *et al.*

1957. Treatise on invertebrate paleontology, Part L, Mollusca 4, Cephalopoda, Ammonoidea. Geol. Soc. Am. and Univ. Kansas Press, 490 pp.

COLOMBO PLAN PROJECT

1961. Reconnaissance geology of part of West Pakistan. Toronto, 550 pp.

DIENER, CARL

1906. Himalayan fossils. Fauna of the *Tropites* Limestone of Byans. India Geol. Surv., Palaeont. Indica, (15) **1**: 1-201, pls. 1-17.

1906. Notes on an Upper Triassic fauna from the Pishin District, Baluchistan, collected by E. Vredenburg in the year 1901. Rec. Geol. Surv. India, **34**: 12-21, pls. 3, 4.

1912. The Trias of the Himalayas. Mem. Geol. Surv. India, **36**: 1-159.

1916. Einige Bemerkungen zur Nomenklatur der Trias-cephalopoden. Centralbl. Mineral. Geol. Paläont., No. 5: 97-105.

HERON, A. M.

1939. General report of the geological survey of India for the year 1938. Rec. Geol. Surv. India, **74**: 1-132.

MOJSISOVICS, E. V.

1896. Beiträge zur Kenntniss der obertriadischen Cephalopoden-Faunen des Himalayas. Denkschr. Akad. Wiss. Wien, **63**: 575-701, pls. 1-22.

1899. Upper Triassic Cephalopoda faunae of the Himalaya. India Geol. Surv., Palaeont. Indica, (15) **3**: 1-157, pls. 1-22.

SPATH, L. F.

1951. Catalogue of the fossil Cephalopoda in the British Museum (Natural History). Part 5, The Ammonoidea of the Trias. London, 228 pp.

VREDENBURG, E.

1904. On the occurrence of a species of *Halorites* in the Trias of Baluchistan. Rec. Geol. Surv. India, **31**: 162-166, pl. 17.

WILLIAMS, M. DEAN

1959. Stratigraphy of the Lower Indus Basin, West Pakistan. Fifth World Petroleum Congress, Sec. 1, Paper **19**: 1-15.

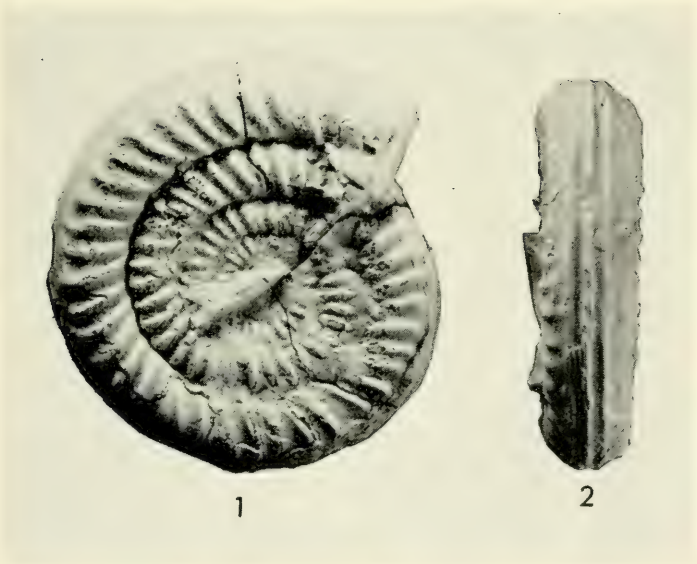

Figure 1. Side and ventral view of *Arietoceltites arietitoides* (Diener) from Triassic formation near Hindubagh, West Pakistan. × 1.

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ADDITIONAL NOTES ON THE AMPHISBAENIDS OF GREATER PUERTO RICO

By RICHARD THOMAS[1]

The overall faunal similarity of Puerto Rico and the Virgin Islands has led to the use of the term "Greater Puerto Rico" for their combined areas (Schmidt, 1928, used the term for a supposed continuous land mass of the past). The amphibaenids of this region have been dealt with thoroughly by Gans and Alexander (1962), in their comprehensive work on the Antillean members of the family. More recently, Gans (1964) has described a new species, *Amphisbaena schmidti*, from Puerto Rico. Thorough as it has been, the work of these authors has been hampered by a dependence upon specimens with insufficient or doubtful locality data.

Herpetological and ornithological collections made under the sponsorship of Dr. Albert Schwartz in the Virgin Islands (summer, 1964) and Puerto Rico (January-March and July 1965, and previous visits) have added new data to the knowledge of the distribution, taxonomy and ecology of the Greater Puerto Rican amphisbaenids with many new specimens and one new species.

PHYSIOGRAPHIC FEATURES OF PUERTO RICO

Before proceeding with the discussion of the species, a brief outline of the major physiographic features of the island of Puerto Rico is pertinent. Puerto Rico may be broken into three general physiographic regions, each of which is, in a broad sense, ecologically uniform.

1. The northern limestone region extends west from roughly the city of San Juan to the western extremity of the island at Aguadilla. This region at its extreme width is one-third that of the island. Most of it is occupied by an extremely eroded topography of close set, conical *mogotes* (to above 1500 feet), often called the Haystack (or Pepino) Hills; but some areas of it are

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Fig. 1. Map of Puerto Rico showing new locality records for *A. caeca* (solid circles), *A. bakeri* (circles with dots), *A. xera* (circles with crosses), and *A. schmidti* (hollow circles). Circles with two half symbols represent sympatric records (only presumptive for Mayagüez). The known range of *A. bakeri* based on previous and present records is indicated by coarse diagonal lines; the range of *A. xera* by fine diagonal lines; and the range of *A. schmidti* by fine horizontal lines. The arrow indicates Caja de Muertos.

rolling or flat, especially along the coastal margin. The termination of this region to the south is usually abrupt and frequently evident as an escarpment. This limestone region varies from xeric to mesic; parts are moist enough for the growing of coffee.

2. The central highlands, primarily igneous in lithology, comprise the main mass of the island and are composed of a very complexly subdivided system of mountains in which few major units or trends are evident. Heights range to over 4000 feet in places, but generally the elevations are moderate (1000-2000 feet). Except for the eastern and western coastal margins it is predominantly mesic and at one time was doubtless almost completely forested.

3. The southern coastal plain is directly continuous with the central highlands but is in contrast ecologically in its aridity. Outstanding faunistically in this region is the area to the south of the Valle de Lajas in the extreme southwest; it is comprised in general of a discontinuous range of low coastal hills, which at one time probably constituted a chain of offshore keys or a peninsula joining the main island in the vicinity of Guayanilla. This southern coastal region, particularly the portion just mentioned, is probably the strongest area of endemism in Puerto Rico, where such forms as *Phyllodactylus wirshingi*, *Sphaerodactylus roosevelti*, *Ameiva wetmorei*, *Anolis poncensis*, *Anolis cooki* (= *A. cristatellus cooki* Grant), and the very distinctive *Typhlops granti* have their primary distributions.

SPECIES DISCUSSION

Amphisbaena bakeri Stejneger

Specimens examined: new localities: PUERTO RICO: 4.2 km S Mora, 500′ (150 m), ASFS V5335; 7 km W Maricao, ca. 300 meters, ASFS V6424. *Previously recorded localities:* "Las Marías," MCZ 66512 (= UPR 1?); "Maricao," MCZ 66513 (= UPR 2?); "Mayagüez," UMMZ 55824.

Amphisbaena bakeri is known only from a few specimens (12 including the new records cited herein) from a cluster of localities in the north-central portion of extreme western Puerto Rico (Fig. 1). The previous localities for this species were all merely town names. From some of the localities were also recorded specimens of *cacca*, but due to the imprecise nature of the localities, it could not be determined whether the two forms were truly sympatric. *A. cacca* was unknown from the northwestern

corner of the island, and the only localities from which it was known "with" *bakeri* were those which were possibly peripheral to the range of *bakeri* (cf. Gans and Alexander, 1962, fig. 4).

A. bakeri differs from the wide-ranging *A. caeca* principally in being larger in size, in having a higher number of body annuli, longer internasal suture, absence of a third row of chin segments, and lack of caudal autotomy (Gans and Alexander, 1962). Only the second (although possibly the third) has been recognized as an absolute difference from *caeca*. The specific distinctness of *bakeri* has therefore not been established with certainty.

One of the recent specimens (ASFS V5335) represents only a minor range extension but constitutes the first record from the northern limestone region; ASFS V6424 is from within the previously known range. There is no evident explanation for the small, very restricted, apparent range of *bakeri*. The fact that a number of specimens of *caeca* (and no *bakeri*) were collected in the vicinity of Utuado indicates that *bakeri* probably does not occur much farther east than it has been previously reported.

The coloration in life of these two specimens of *A. bakeri* was noted as being "pale pinkish gray"; ASFS V6424 was noted as being "pink below" (ventrally). The right hemipenis of ASFS V6424 is everted and appears to be very similar to the hemipenis of *A. caeca* (Fig. 2).

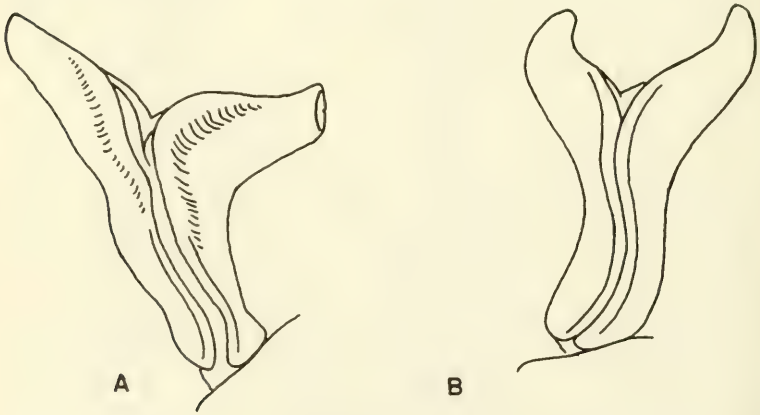

Fig 2. Hemipenes of *A, Amphisbaena schmidti* (ASFS V5871), and *B, Amphisbaena caeca* (ASFS X4111); view cephalad with organs normal to body axis.

ASFS V5335 from the northern limestone region was collected in a small grassy pasture, which formed the bottom of a doline in a mesic portion of the Haystack Hills. It was found beneath a rock where it was seen disappearing into a vertical burrow in moist clayey soil from which it had to be dug. ASFS V6424 was taken in a typical coffee producing area of the central highlands. It was found in a rotten log along the edge of a clearing overgrown with short, weedy vegetation. The nature of the ecological preferences of *bakeri* cannot, of course, be judged from just two encounters. The locality for the first specimen (4.2 km S Mora) is clearly within the range of *caeca,* the nearest locality for that species being less than three kilometers to the south. *A. schmidti* also occurs in this part of the limestone hills; the nearest locality for that species was 0.2 kilometers to the north of the locality for the first specimen of *bakeri.* Thus, in this area, the three known Puerto Rican species occur sympatrically, whatever their ecological preferences (see below for *caeca* and *schmidti*).

Amphisbaena caeca Cuvier

Specimens examined: new localities: PUERTO RICO: 13.3 km E Utuado, ASFS V4443-48; 17.7 km NE Utuado (= approx. 8 km straight line distance), 1100′ (335 m), ASFS V4482, V4499, V4500-01, V4623, V4449, V5860; 8 mi. (13.5 km) NW Utuado, 1500′ (407 m), ASFS V4548; 9 mi. (15 km) E Lares, ASFS V4656; 7.0 km S Mora, 800′ (244 m), ASFS V5152, V5329, V5332; 5 mi. (8 km) NE Lares, 1200′ (366 m), ASFS V5267; Ramey Air Force Base, Rifle Range Beach, ASFS V5430-31; 2.3 km E Juana Díaz, 200′ (61 m), ASFS V5755; 3 km NE San Germán, ASFS V6407; 4.6 km W, thence 4.6 km NW Juana Díaz, ASFS V6620-28, V6631-35; 3.6 km W, thence 9.7 km N Juana Díaz, ASFS V6658-59; 3.6 km W, thence 8 km N Juana Díaz, ASFS V6660-61; 10.2 km E Dos Bocas, ASFS V5861-62; 18.8 km SW Arecibo, 800′ (244 m), ASFS V5908-09; 11.2 km NW Utuado, 1300′ (400 m), ASFS V5922; 1 mi. (1.6 km) NW Dorado, ASFS V5939; 4.1 km NE Villa Pérez, 2200′ (670 m), ASFS V5973; 2 km NE Barranquitas, 2100′ (640 m), ASFS V6027; 1.8 km S Adjuntas, ASFS V6207; 12.3 km SE Patillas, ASFS V4798; 10 km SE Patillas, ASFS V4802; 12.9 km SW Fajardo, 800′ (244 m), ASFS V5081. VIEQUES: Cayo de Afuera, ASFS V6168. *Previously recorded localities:* PUERTO RICO: Isla Verde, ASFS X937-43, X4104-

25, X7381-98; 2.2 mi. SW Sabana, ASFS X7433-34; Mayagüez, UPR 84c, 87, 88, 90, 92, 140.

Large numbers of *A. caeca* were examined by Gans and Alexander, but they had large series from the eastern part of the island only and relatively few specimens from the west. The species was not then known from the northwestern corner, an area bounded roughly by Mayagüez, Lares and Arecibo. The present collection also has an eastern bias due to the large series from Isla Verde, but a more thorough coverage has been made in the west, including the formerly blank northwest portion.

With the new material I have not undertaken a detailed analysis of trends such as that done by Gans and Alexander (fig. 29). However, I have compared trends in number of body annuli of selected eastern (Isla Verde and east), central (Juana Díaz region), west central (Utuado-Adjuntas region), and western (Ramey Air Force Base to south of Mora) "samples" (these do not include all specimens examined) with those shown by Gans and Alexander for this character (in which the strongest trends were evident). An agreement in direction of trends was found. Both pre- and postcloacals average fewer in eastern specimens; this is also in agreement with the observations of Gans and Alexander. Additionally, internasal suture length (expressed as a fraction of interprefrontal suture length) averages longer in the eastern specimens.

The largest specimen (ASFS V6207) is a male that measures 291 mm total length (tail 21 mm), which appears to be the largest *caeca* recorded (the largest seen by Gans and Alexander was 269 mm total length). A body annulus count of 214 (ASFS V4120) is lower than the low value of 217 recorded by Gans and Alexander.

The Vieques specimen is, in a way, the first record for that island. The specimen was not taken on the main island but on an offshore key, Cayo de Afuera. However, the species may be assumed to occur on Vieques proper. It has long been a matter of speculation as to which species of *Amphisbaena* would be found on Vieques and Culebra, *caeca* or *fenestrata*. Some have tacitly assumed the former. Of course, the finding of one species does not preclude the possibility that the other might also occur on the island. The Cayo de Afuera specimen has a high number of ventral midbody segments; it is also near the upper extreme of *caeca* in body annuli.

A. cacca seems to prefer a mesic, usually shady, habitat (see below for comparisons with other species); it occurs from montane *cafetales* at elevations of at least 2200 feet (ASFS V5973, apparently the highest elevation record for *cacca*) to the coast. It still appears to be absent from the extremely arid southern regions; the record of Fowler (1918) for Guánica probably does not pertain to this form (*vide infra*). One specimen (ASFS V4798) was collected approximately 40 feet from the ocean's edge and shed skins were found in the vicinity. Three specimens were collected in rotting wood, two in logs that were not even in firm contact with the ground. The most xeric habitat in which I have found *cacca* was on Cayo de Afuera; even there it was in a wooded and somewhat shady, although not moist, situation.

Amphisbaena xera new species

Holotype: MCZ 81019, an adult male from 7 km E of Guánica, Puerto Rico, elevation 600′ (183 m), one of a series collected on 6 March 1965 by Albert Schwartz and Richard Thomas.

Paratypes: PUERTO RICO: UIMNH 56910, ASFS V5646, USNM 152588, 7.3 km E Guánica, 2 March 1965, R. Thomas; ASFS V5659, 7.1 km E Guánica, 3 March 1965, R. Thomas; ASFS V5662, 7.3 km E Guánica, 3 March 1965, R. Thomas; ASFS V5722-23, AMNH 94170, same data as type (foregoing localities are at the same elevation as that of the type); UMMZ 73844, Sabana Grande; ASFS V5800, 6.2 km E Juana Díaz, 10 March 1965, R. Thomas; ASFS V6408, 5 mi. (8 km) ESE San Germán, south slope Cerro Algarrobo, 9 July 1965, R. Thomas; ASFS V6148, 5 mi. (8 km) ESE San Germán, south slope Cerro Algarrobo, 10 July 1965, R. Thomas; ASFS V6423, 1.5 km WNW San Germán, 11 July 1965, R. Thomas; ASFS V6427, 3 km NE San Germán, 12 July 1965, R. Thomas; ASFS V6587, 2.3 km E Juana Díaz, 26 July 1965, R. Thomas; ASFS V6616-18, 4.6 km W, thence 1.1 km NW Juana Díaz, 27 July 1965, R. Thomas; ASFS V6619, 4.6 km W, thence 4.6 km NW Juana Díaz, 27 July 1965, R. Thomas; ASFS V6636-40, 28 July 1965, R. Thomas; ASFS V6646-57, 4.6 km W, 1.9 km NW Juana Díaz, 28 July 1965, R. Thomas; CM 40577-78, RT 1333-34, 4.6 km W, thence 1.9 km NW Juana Díaz, 29 July 1965, R. Thomas; UMMZ 73846, 3 mi. (4.8 km) E Juana Díaz, 27 November 1931, Chapman Grant; MCZ 36301, 10 mi. (16 km) E Juana Díaz, 27 November 1931, C. Grant; UPR 84a-b, Mayagüez, 10

December 1957, J. A. Ramos; UPR 86, Mayagüez, 8 September 1949, Nestor Nazario; UPR 91, no data.

Diagnosis: A form of *Amphisbaena* lacking fusion of head scales, of closest affinities to the species *bakeri* and *caeca*, differing from the former in having a low number of body annuli (225-234), the presence of a third row of chin segments (most specimens), and much smaller size. From *caeca* it differs in possessing a relatively longer internasal suture (32 to 53 per cent of the length of the interprefrontal suture), lack of a postmalar row of chin segments, fewer average midbody segments, caudal autotomy absent or ill-defined, and smaller size.

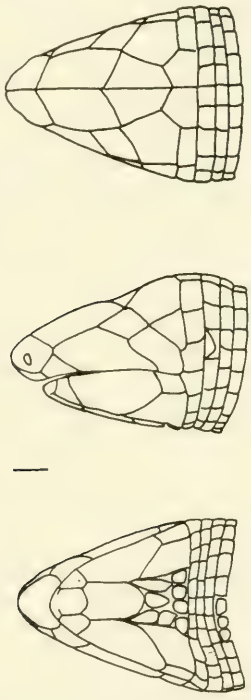

Fig. 3. Dorsal, lateral and ventral views of the head of the type of *A. xera* (MCZ 81019). Line represents 1 mm to scale.

Description of type (Fig. 3): Meristic and mensural data for type and paratypes are found in Table 1. The type is a mature adult male with the hemipenes partially everted. The first two body annuli correspond to three dorsal half-annuli; the median

segments of the second dorsal half-annulus are enlarged to form a pair of parietals in broad contact at the midline; the median segments of the third dorsal half-annulus are not enlarged to form a second pair of parietals. In the chin region two of the three segments of the first postgenial row are fused with two in the second row so that the second row is represented by only one segment (Fig. 3); the mental is partly fused with the genial. The postmalar[1] row contains four scales and is bounded laterally by the malars which abut on the first body annulus. The dorsal groove is weakly indicated by an alignment and some medial rounding of the posterior paravertebral segments.

Variation: In size, only five specimens exceed the type; 42 (90 per cent) are smaller. The head scalation described for the type is characteristic; a second pair of parietals is indicated in only four specimens. The internasal sutures range from 32 to 53 per cent of the length of the interprefrontal sutures. In the chin region the most variability is encountered in the second row of postgenials. Its scales are often variously fused with the first and third rows, or it may be represented only by one or two small and irregular scales crowded between the first and second rows. Eighteen specimens have only two postgenial rows and thereby have the chin configuration of *bakeri*. It is as if the second postgenial row were being lost. The lack of a postmalar row is characteristic; one specimen (ASFS V6637) appears to have this row but the malar is abnormally divided. Autotomy constrictions are evident in a few specimens at the level of the fifth to seventh caudal annulus; slightly heavier pigmentation of a caudal annulus may mark the autotomy level in others. Other specimens either definitely do not have an autotomy constriction or the presence of one is indeterminate. Cloacal pores are four, with the exception of one specimen which lacks two on one side. Hemipenes are very similar to those of *bakeri* and *caeca* (Fig. 2).

Coloration: The dorsal coloration in life of this form is typically a pale tan, very reminiscent of the two living specimens of *bakeri* I have seen. The coloration lightens gradually towards the ventral surface and pigmentation is almost absent on the four ventralmost rows. Dropping out of pigmented ventral segments takes place in some specimens but is not prominent because of the fading out of all pigmentation ventrally. Dorsally

[1] I have objected elsewhere (Thomas, 1965) to the use of the term postmalar; however, this was due to my misunderstanding of the terminology as it applied to *Amphisbaena innocens*.

and ventrally the coloration is darker (browner) anteriorly. In life the venter is pink due to the translucence resulting from lack of pigmentation. The temporal region is deep reddish purple, probably another product of superficial vascularity and pigmentation. The snout (including prefrontals) is light (buffy) as is the posterior half of the edge of the lower jaw.

Comparisons and discussion: The most pertinent comparisons of *xera* are with *caeca* and *bakeri* (Fig. 4). Seven specimens, having no postmalar row of chin segments and regarded by Gans and Alexander as *A. caeca*, are here regarded as *A. xera*. Aside from one specimen I have not seen (SU 7775, examined by Gans and Alexander) which may also be referable to *xera*, and a possible exception noted above, the absence of a postmalar

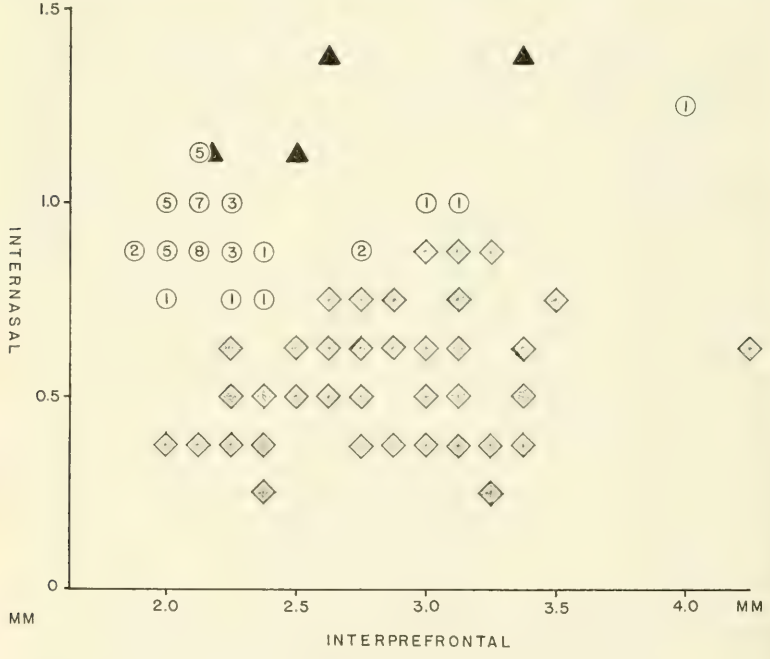

Fig. 4. Scatter diagram of internasal versus interprefrontal suture lengths for *A. caeca* (stippled squares), *A. bakeri* (solid triangles), and *A. xera* (hollow circles). Numbers in the *xera* symbols indicate the number of specimens possessing that value. Values were not plotted for all specimens of *caeca* examined, only enough to show variation including extremes. The symbols at the extreme right for *xera* and *caeca* represent the values for the largest specimen of each of these two forms.

row distinguishes *xera* from *caeca* in all cases. Internasal suture length varies from 32 to 53 per cent of the interprefrontal suture in *xera;* in *caeca* the longest interprefrontal sutures (29 per cent of the interprefrontal length) are found in four specimens from eastern Puerto Rico, where the internasal suture length averages higher than in material from the rest of the island (and interestingly an area where sympatry with the two other long internasal suture forms is absent). *A. xera* is characterized by a low number of segments around midbody; one specimen (from Mayagüez) has 32 midbody segments, otherwise the range is 26 to 30; a count of 30 or below is found in less than 20 of over 300 specimens of *caeca* examined by Gans and Alexander and by me. In the low average number of cloacal scales *xera* is more like eastern *caeca* than like those from other parts of the island. In coloration *xera* is paler than most specimens of *caeca* which are typically brown or gray-brown rather than pale (or even reddish) tan (although this color does occur in *caeca*). Specimens of *xera* are usually identifiable on first sight by their paler color and more slender proportions (*caeca* is characteristically stouter, doubtless a correlative of the greater number of midbody segments). The tails are tapered towards the tip and are not so cylindrical and rounded terminally as is typical of *caeca;* this is a distinguishing character in living specimens. The pale snout of *xera* is also not found in *caeca* (or is not so extensive).

A. caeca and *A. xera* are allopatric for the most part; they have been taken together at four localities (Mayagüez, 3 km NE San Germán, 4.6 km W, thence 4.6 km NW Juana Díaz, 2.3 km E Juana Díaz), all peripheral to the range of *xera* and apparently to that of *caeca.* At these localities there is no evidence of intergradation. Relatively short internasal sutures are found in the four Mayagüez *xera* and in the one from Sabana Grande (30 to 33 per cent of the length of the interprefrontal suture), but these do not overlap with internasal suture lengths for *caeca* from any part of the island. One Mayagüez specimen (UPR 84a) has 32 segments at midbody (16/16), the only *xera* with counts higher than 30.

A. xera is strikingly like *bakeri* in several respects (internasal suture, lack of caudal autotomy, lack of a postmalar row, pale coloration), although in others it is significantly different (fewer body annuli, size, gradual fading of color on venter). In size, 9 of the 12 known specimens of *bakeri* are larger than 42 (90 per cent) of the specimens of *xera.* The configuration of the chin segments may well be thought of as intermediate between the

conditions in *bakeri* and *cacca* but tending more towards the former. The 18 *xera* with but two postgenial rows are even more suggestive of a trend towards *bakeri*.

Schmidt (1928) commented on three specimens from Mayagüez that appeared to be intermediate between *bakeri* and *cacca*. Two of these (noted as having an internasal length of about one-half the interprefrontals) almost certainly pertained to *A. xera* (these specimens do not appear to be extant). The other specimen (CNHM 12473) was identified by Gans and Alexander as *A. bakeri*. Two specimens of *bakeri* are known from Mayagüez; one (CNHM 12473) has a body annulus count of 240, which is near the extreme low for that form; another has a count of 255 which is at the upper extreme. A specimen (UPR 7, Gans and Alexander), which has no locality data other than Puerto Rico, is probably from the Mayagüez region; it has a body annulus count of 239. It should also be recalled that three of the Mayagüez (and the one from Sabana Grande) specimens are at the upper extreme in size for *xera*. More specimens with precise data from the Mayagüez vicinity may show that *bakeri* and *xera* are subspecifically related. I am reluctant to so allocate these forms now because *bakeri* is so little known.

A. schmidti is distinguished from *xera* by its lower number of body annuli (192-207 versus 225-234), higher number of caudal annuli (18-22 versus 10-14), the presence of caudal autotomy, larger size, different proportions, and overall darker coloration. The two are additionally distinguished by differences in relative size of some of the head scales and by different chin segment configurations.

Range: Known from the central to western parts of the southern xeric coastal plain of Puerto Rico (Fig. 1) and as far north as Mayagüez, San German, Sabana Grande, and to the northwest of Juana Díaz. In all probability it occurs on Caja de Muertos,[1] whence there are shed skins yielding midbody segment counts of 14/16 (1) or 14/14 (2) and caudal annuli of 12 (2), 13 (1) or 14 (1). The specimen recorded by Fowler (1918) from Guánica may well have been of this new form.

Habitat: The topotypical paratypes and type (7.0-7.3 km E Guánica) were collected in the xeric woods which form the more luxuriant covering of the limestone hills of this region.

[1]Heatwole, Torres and Heatwole (Stahlia, 1965, no. 4, p. 1) recorded taking a specimen of *Amphisbaena* on Caja de Muertos. I have not examined this specimen, but almost certainly it pertains to *A. xera*, as it was noted to lack the postmalar row of chin segments and also agreed with *xera* in other counts given.

The soil varied from sandy with moderate organic (plant) content to loamy; there was a uniform cover of leaf litter. At the type locality, *A. xera* occurs syntopically with *Typhlops richardi* and *Typhlops granti*.

The specimen from 6.2 km E Juana Díaz was collected in a region of xeric foothills; it was found at night under a rock which was not at all imbedded in the soil. The area was exposed and had very sparse vegetation. In the heat of the day it was doubtless a most inhospitable place, and the chance of finding an *Amphisbaena* near the surface would have been negligible.

At the following three localities I was able to personally collect and observe *caeca* and *xera* together.

3 km NE San Germán. This locality is in the foothills to the north of the San Germán valley; it is transitional between the arid region to the south and the mesic highlands, but closer to the latter. The single specimen of *caeca* was collected on a boulder-strewn and somewhat wooded hillside surrounded by pasture; the specimen of *xera* was collected near a small stream at the base of the hillside. No ecological differences were discernible.

4.6 km W, thence 4.6 km NW Juana Díaz. This locality is in the valley of the Río Inabón; it too is transitional between the xeric south and the mesic interior. On the first visit, nine specimens of *caeca* and one of *xera* were found in a patch of sandy, mesic, river-border woods. The surrounding regions (where natural growth was evident) were covered by semi-arid scrubby woods; the spiny palm (*Acrocomia*), a typically semi-xeric form, was seen on some of the nearby hillsides. On the second visit an attempt was made to collect in a more open, scrubby, overgrown field nearby. Five specimens of *xera* and five of *caeca* were obtained. Not quite three kilometers to the south, another area of shady (but distinctly more xeric) riverine woods was visited. Eighteen specimens of *xera* (two of which have not been examined for this paper) were collected and no specimens of *caeca*. Less than a kilometer more to the south in still arid country, three more specimens of *xera* but no *caeca* were taken.

2.3 km E of Juana Díaz. This locality is a mesic, wooded ravine surrounded by typically xeric to semi-xeric regions. One specimen each of both species was found in the ravine.

Amphisbaena schmidti Gans

Specimens examined: new localities: PUERTO RICO: 5.5 mi. (9 km) N Lares, 1100′ (346 m), ASFS V5197-99, V5258-60; 5 mi. (8 km) NE Lares, 1200′ (366 m), ASFS V5268; 4 km S Mora, 500′ (153 m), ASFS V5334; Ramey Air Force Base, Rifle Range Beach, ASFS V5432-37; 3 mi. (4.8 km) W Las Llanadas, 600′ (183 m), ASFS V5871; 18.8 km SW Arecibo, 800′ (244 m), ASFS V5910; 11.2 km NW Utuado, 1300′ (400 m), ASFS V5923-24; 1 mi. (1.6 km) NW Dorado, ASFS V5940; 3.5 mi. (5.4 km) W Playa de Vega Baja, ASFS V5959; 2.5 km SW Florida, ASFS V5999; 5.6 km NE Morovis, 400′ (122 m), ASFS V6028-29.

Amphisbaena schmidti was described (Gans, 1964) on the basis of six specimens from four more or less coastal localities, three in the northwest section of the island and one ("Salinas") presumably on the south coast. Professor Manuel J. Vélez, collector of the type and one paratype of *schmidti,* has informed me (*in litt.*) that the type locality of *A. schmidti* should correctly be "Isabela, orilla (cuneta) Carretera Caño." The locality is in the district of Isabela about six kilometers southeast of the town of Isabela by the side of Carretera Caño (= road number 113).

The distribution of *schmidti* was given as "coastal Puerto Rico." The new localities cited here are restricted to the northern limestone section (up to elevations of 1300 feet), and the species is in all likelihood endemic to this region (Fig. 1). No specimens were found elsewhere on the island.

Of the numbers of amphisbaenids collected in the southern part of Puerto Rico (*A. caeca* and *A. xera*) and of the shed skins that were often found there, none pertained to *A. schmidti.* The apparent absence of *schmidti* from the southern marginal region plus its absence from the coastal regions east of San Juan (in spite of the large series of *caeca* from there) indicate that its distribution is not coastal Puerto Rico and, at the same time, throw considerable doubt on the Salinas record. Conceivably it refers to another Salinas (a not uncommon coastal name in Latin America), possibly Punta Salinas on the north coast to the west of San Juan, which is probably in the range of *schmidti.*

The new specimens of *schmidti* agreed in coloration (in life) very closely with the coloration recorded by Gans; they were usually noted as being purplish brown dorsally with darker

brown heads and tails. The venters are heavily pigmented but sometimes pinkish. In general proportions and appearance this species is very distinct; the blunted and almost triangular head is characteristic and is accentuated by the deeply constricted neck. Indeed, this species, in proportions, color and scutellation, is possibly the most "different" of the species of the Greater Puerto Rican region. The enlarged parietals and enlarged scales at the end of the third row of chin segments are very characteristic.

Completely everted hemipenes (Fig. 2) are present in two specimens. The organs are relatively slender and deeply bilobed; the sulcus spermaticus forks in the crotch, and the apices are flattened, a condition that has been noted for *innocens* and not for *caeca* which has rounded apices (Thomas, 1965). Autotomy level varies from the sixth to eighth caudal annulus.

Different ecological preferences were observed for *schmidti* and *caeca* in the jointly occupied parts of their ranges. *A. schmidti* was found in more open and exposed areas, the edges of pastures, the cleared sides of gradually sloping dolines — areas where the tree cover is lacking, or high and sparse. *A. caeca*, although wider in its ecological range, prefers shady areas such as coffee groves or wooded ravine bottoms. The following table indicates briefly the type of situation in which either species was collected at particular localities within their joint range; the number of specimens at each locality is indicated in parentheses.

schmidti	*caeca*
acacia scrub (6)	coastal almond (*Terminalia*) woods (2)
moderate to well-exposed, scrubby ravine sides (6)	. . . . .
moderately exposed hillside (1)	. . . . .
. . . . .	coffee grove (3)
. . . . .	coffee grove (1)
exposed hillside pasture (2)	mesic woods adjacent to pasture (1)
high, open ravine woods (1)	exposed ravine side (1), shady ravine woods (1)
moderately exposed edge of coffee grove (1)	interior of coffee grove (1)

schmidti	*caeca*
guava scrub at rim of doline pasture (1)	.....
.. ..	in coffee grove (2)
moist, open pasture (2)	.....
cleared slope of doline (1)	.....
moderately exposed roadside ditch (1)	shady coastal woods (1)
open lake margin (1)	.....

AMPHISBAENA FENESTRATA Cope

Specimens examined: new localities: VIRGIN ISLANDS. *St. John:* Lameshur Bay, VINP 1478; Annaberg Road near Frederickdal, VINP 1479; Caneel Hill Trail, VINP 1485; Coral Bay, VINP 1490; Windberg ruins, ASFS V7504-05; Frederickdal ruins, ASFS V7564, V8066. *Tortola:* Baugher's Bay, ASFS V7921; Jackass Gut, ASFS V7940, V7984-85, RT 977. *Virgin Gorda:* SW slope of Gorda Peak, ca. 500′ (150 m), ASFS V3805-06. *Great Camanoe:* between Lee Bay and Cam Bay (shed skin). *Previously recorded localities: St. John:* VINP 1496-97.

In the report on *A. fenestrata* by Gans and Alexander, "Dorothea" and "West End of Great St. James" are listed in "locality records" under St. John. Dorothea is on St. Thomas and Great St. James is a small satellite island of St. Thomas.

When the data from the new specimens are placed with the old data from the various islands, the trends noted by Gans and Alexander are almost completely obliterated. The following ranges summarize the new data (data from Gans and Alexander are in parentheses):

Island	body annuli	caudal annuli	ventral segments	posteloacals
St. Thomas	..... (242-247)	.... (12-14)	.... (14-16)	... (8-10)
St. John	241-251 (247-249)	12-13 (12-14)	14-17 (14-15)	8-11 (9-10)
Tortola	243-248 (236-242)	13-14 (13-14)	14-16 (14-16)	8-11 (9-12)
Virgin Gorda	240-245	12-13	16-17	9 ...

The shed skin from Great Camanoe is too fragmentary to yield counts. The Virgin Gorda and Great Camanoe records are the first for those islands. The two specimens from Virgin Gorda have higher dorsal midbody counts than do those of the other islands; the total midbody counts are higher than all but one of the specimens from the other islands.

Gans and Alexander have said (1962:95) that the dorsal groove in West Indian *Amphisbaena* "may be suggested by an alignment alone." However, in well-injected specimens of *A. fenestrata* the dorsal groove is structurally evident on approximately the posterior two-thirds to three-fourths of the body. The paramedian segments are rounded medially and the resulting space is occupied by "fold granules." The appearance of this groove at its fullest development is much the same as that of the lateral grooves. It becomes increasingly indistinct anteriorly and ends at the approximate level of the thirty-sixth to sixty-seventh postoral annulus. No other specimens of West Indian species seen by me (*cacca, schmidti, bakeri, cubana, innocens, gonavensis, manni*) have so prominent a dorsal groove, although one specimen of *bakeri* has a moderately well indicated dorsal groove.

Amphisbaena fenestrata inhabits islands that are preponderantly xeric; however, it prefers (or at least is most easily collected in) the most mesic areas that can be found. When we visited Virgin Gorda the weather was unseasonably dry. Shed skins of these animals were found regularly under rocks in the more shady parts of the low, xeric woods that cover much of the island. After almost a week of persistent rock turning, two specimens were obtained on a heavily wooded hillside after a heavy morning shower. *Typhlops richardi,* which was more abundantly collected in all parts of the island, was also found in moist piles of coconut husks near the coast, where *Amphisbaena fenestrata* was not. This preference for the more mesic areas was noticed also on St. John and Tortola. The presence of a soil of high organic content seems to be an important factor. A brief visit to the island of Anegada yielded no specimens or signs of amphisbaenids, although six specimens of *Typhlops* were collected.

This species is now known from the islands of St. Thomas, Great St. James, St. John, Tortola, Great Camanoe, and Virgin Gorda. Its true range is probably all of the Virgin Islands large enough to bear a suitable habitat, St. Croix excepted. Anegada is geologically distinct and well set off from the rest of the Virgins, but its fauna is not radically different; *fenestrata* may be found there.

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LITERATURE CITED

Gans, Carl

1964. *Amphisbaena schmidti*, a third species of the genus from Puerto Rico (Amphisbaenia, Reptilia). Breviora, Mus. Comp. Zool., No. **198**, pp. 1-11.

Gans, Carl and A. Allan Alexander

1962. Studies on amphisbaenids (Amphisbaenia, Reptilia). On the amphisbaenids of the Antilles. Bull. Mus. Comp. Zool., Vol. **128**, no. 1, pp. 65-158.

Fowler, Henry W.

1918. Some amphibians and reptiles from Porto Rico and the Virgin Islands. Pap. Dept. Marine Biol. Carnegie Inst., vol. **12**, pp. 1-15.

Schmidt, Karl Patterson

1928. Amphibians and land reptiles of Porto Rico, with a list of those reported from the Virgin Islands. Sci. Surv. Porto Rico and Virgin Islands, vol. **10**, part 1, pp. 1-160, 4 pls.

Thomas, Richard

1965. Two new subspecies of *Amphisbaena* (Amphisbaenia, Reptilia) from the Barahona Peninsula of Hispaniola. Breviora, Mus. Comp. Zool., No. **215**, pp. 1-14.

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KEY TO GREATER PUERTO RICAN SPECIES OF *AMPHISBAENA*

1. Nasals separated by posterior extension of rostral which contacts prefrontals; body annuli 236-249 ..... *fenestrata*
   Nasals in contact with one another 2

2. Number of body annuli low (192-207); high number of caudal annuli (18-22) ..... *schmidti*
   Number of body annuli higher (more than 214); caudal annuli lower (17 or less) 3

3. Internasal suture short (less than one-third interprefrontal suture); body annuli 214-237 ..... *caeca*
   Internasal suture long (one-third or more the length of interprefrontal suture) 4

4. Number of body annuli higher (239-255); size large ..... *bakeri*
   Number of body annuli lower (225-237), size small ..... *xera*

TABLE 1

Meristic and mensural data for specimens of *Amphisbaena* examined. Tail and total length measurements are in millimeters. Internasal and interprefrontal suture lengths are in ocular micrometer units; one unit equals 0.125 mm. Asterisks indicate abnormality or autotomized tails.

SPECIMEN NUMBER	ANNULI BODY	SEGMENTS LATERALS	CAUDAL	DORSAL	VENTRAL	POSTGENITALS	POSTMALARS	PORES PRECLOACALS	POSTCLOACALS	INTERNASAL SUTURE	INTERPREFRONTAL SUTURE	TOTAL LENGTH	TAIL LENGTH
A. BAKERI													
ASFS V5335	251+	4	+12	16/16	3	4	- -	4+7+11		9	20	243	12
ASFS V6424	255+	3/4	+14	14/16	3	4	- -	4+6+10		9	20	236	15
MCZ 66512	253+	4	+13	16/17	3	4	- -	4+6+11		11	21	269	17
MCZ 66513	245+	4	+13	16/18	3	5	- -	4+8+11		11	27	322	20
UMMZ 55824										9	17		
A. CAECA													
ASFS V5430	229+	3	+14	16/16	3	4	- 9	4+6+14		3	22	231	15
ASFS V5431	226+	3	+14	16/16	3	4	- 9	4+6+12		4	22	196	13
UPR 84c	227+	3	+15	16/16	3	3	5 9	4+8+13		4	24	193	13
UPR 87	229+	3	+16	14/16	3	4	- 9+10*	4+8+13		5	22	215	18
UPR 88	223+	3	+15	17/18	3	4	- 9	4+7+11		4	28	198	14
UPR 90	227+	3	+15	16/17	3	4	- 8	4+6+13		4	26	196	14
UPR 92	225+	3	+6*	16/17	3	4	- 9	4+8+12		5	23		
UPR 140	228+	3	+15	16/16	3	4	- 9	4+6+12		5	21	170	13
ASFS V5152	234+	3	+14	16/18	3	4	- 8	4+8+13		3	23	206	14
ASFS V5329	233+	3	+15	16/18	3	2	- 8	4+8+12		6	24	202	11
ASFS V5332	231+	3	+15	16/18	3	4	- 8	4+8+12		6	24	225	15
ASFS V5305	232+	3/4	+14	16/16	3	4	- 9	4+8+12		4	21	186	13
ASFS V5267	225+	3	+5*	16/18	3	4	- 9	4+8+12		4	24	206	7*
ASFS V6407	216+	3	+16	17/16	3	4	- 9	4+8+12		4	19	172	14
ASFS V5908	227+	3	+5*	16/18	3	4	- 9	4+7+12		3	25	218	7*
ASFS V5909	221+	3	+15	16/18	3	4	- 8	4+8+12		3	19	160	13
ASFS V4656	221+	3	+15	16/16	3	4	- 9	4+6+12		2	26	217	17
ASFS V4548	229+	4	+15	16/17	3	4	- 9	4+8+13		3	25	225	16
ASFS V5939	227+	3	+14	15/17	3	4	- 9	4+8+11		4	24	215	16
ASFS V5973	232+	3	+5*	15/18	3	1*	- 6*	4+6+12		4	20	148	5*
ASFS V6207	231+	3	+14	16/17	3	3	- 8	4+6+13		5	34	291	21
ASFS V4443	232+	2/3	+14	14/16	3	5	- 10	4+6+12		3	18	241	16
ASFS V4444	233+	3	+15	16/17	3	4	- 9	4+7+13		4	27	231	16
ASFS V4445	234+	2/3	+15	16/16	3	4	- 9	4+7+12		3	26	210	14
ASFS V4446	232+	3	+14	17/17	3	6	- 9	4+8+13		4	27	224	16
ASFS V4447	235+	3	+15	16/18	3	4	- 10	4+8+13		4	24	195	13
ASFS V4448	230+	3	+14	14/16	3	5	- 8	4+6+13		4	21	174	12
ASFS V4449	232+	4	+15	14/16	3	3	- 7	4+7+12		4	24	210	16
ASFS V4482	230+	3	+15	16/17	3	4	- 9	4+7+14		4	21	165	11
ASFS V4499	231+	3	+6*	14/16	3	4	- 8	4+7+13		4	27	226	7*
ASFS V4500	230+	3	+15	14/16	3	4	- 9	4+8+12		4	26	230	14
ASFS V4501	229+	2/3	+14	15/16	3	4	- 8	4+8+14		4	21	171	11
ASFS V4623	231+	3/3	+15	15/16	3	4	3* 9	4+8+13		3	24	198	15
ASFS V5860	234+	3	+15	16/18	3	4	- 8	4+8+12		3	26	209	15
ASFS V5861	235+	3	+14	14/16	3	4	- 9	4+8+13		4	20	160	10

ASFS V5862	226+2/3+15	14/16	3	4	-	9	4+8+12	4	19	148	9
ASFS V6620	223+2/3+14	16/16	3	4	-	9	4+7+14	5	27	227	17
ASFS V6621	223+ 3 +14	16/16	3	4	-	9	4+6+12	3	27	218	15
ASFS V6622	219+ 3 +14	16/16	3	4	-	9	4+8+12	6	23	205	15
ASFS V6623	220+ 3 +14	16/17	3	4	-	9	5+8+14	2	19	205	14
ASFS V6624	226+ 3 +12	17/16	3	4	-	9	4+8+12	4	25	197	13
ASFS V6625	219+2/3+13	18/18	3	4	-	7	4+7+12	4	25	196	14
ASFS V6626	221+ 3 +14	16/16	3	4	-	9	4+8+12	5	22	145	14
ASFS V6627	221+ 3 +13	16/16	3	2	-	7	4+6+12	4	24	193	12
ASFS V6628	224+ 3 +13	16/16	3	4	-	9	4+7+13	5	23	185	13
ASFS V6631	220+ 3 +14	16/16	3	4	-	9	4+6+13	5	27	218	16
ASFS V6632	222+ 3 +14	16/16	3	4	-	9	4+7+13	4	25	202	14
ASFS V6633	222+ 3 +14	16/16	3	4	-	8	4+7+12	5	23	202	15
ASFS V6634	219+ 3 +14	16/16	3	4	-	8	4+8+12	4	24	177	13
ASFS V6635	223+2/3+14	16/16	3	4	-	9	4+8+12	5	23	191	14
ASFS V6658	220+ 3 +13	16/18	3	4	-	10	4+8+13	5	18	227	16
ASFS V6659	220+ 2 +14	16/18	3	4	-	10	4+8+13	5	23	185	13
ASFS V6660	223+ 3 +14	16/16	3	5	-	9	4+6+13	6	25	215	15
ASFS V6661	222+ 2 +14	16/18	3	6	-	10	4+7+12	6	23	210	15
ASFS V5755	225+ 4 +14	17/18	3	4	-	10	4+8+12	6	23	199	13
ASFS V5939	223+ 4 +14	14/16	3	3	-	7	4+7+13	4	23	208	14
ASFS V6027	226+3/4+12*	18/18	3	4	-	8	4+8+12	4	24	220	17
ASFS X937	224+ 4 +12	16/18	3	4	-	9	4+6+12	6	28	245	15
ASFS X938	222+ 4 +12	16/18	3	4	-	9	4+6+12	4	24	221	15
ASFS X939	226+ 3 +13	16/18	3	4	-	9	4+7+13	5	23	208	15
ASFS X940	223+3/4+13	17/18	3	4	-	9	4+6+13	5	25	214	15
ASFS X941	229+ 3 +14	16/16	3	4	-	9	4+6+12	5	24	207	14
ASFS X942	220+ 4 +13	16/18	3	4	-	9	4+6+12	4	20	177	12
ASFS X943	224+2/3+14	15/16	3	4	-	9	4+8+11	4	18	109	7
ASFS X4104	222+ 3 +14	16/17	3	4	-	9	4+6+10	4	22	214	16
ASFS X4105	225+ 4 +13	16/18	3	3	-	6	4+7+10	6	23	222	16
ASFS X4106	228+ 3 +14	16/18	3	4	-	9	4+6+12	4	23	220	15
ASFS X4107	229+ 4 +15	16/16	3	3	-	9	4+6+13	5	25	226	17
ASFS X4108	220+ 3 +13	14/16	3	4	-	9	4+6+12	6	24	205	14
ASFS X4109	223+ 3 +14	16/18	3	4	-	9	4+6+10	5	23	199	14
ASFS X4110	218+ 3 +14	16/18	3	4	-	8	4+6+13	6	23	220	16
ASFS X4111	230+3/4+13	16/16	3	4	-	8	4+6+11	7	24	227	16
ASFS X4112	223+3/4+13	16/16	3	5	-	9	4+6+12	4	24	201	13
ASFS X4113	218+ 3 +14	16/18	3	4	-	9	4+6+11	4	23	203	15
ASFS X4114	228+3/4+14	16/18	3	4	-	8	4+6+13	5	22	197	14
ASFS X4115	228+ 4 +13	16/18	3	4	-	8	4+6+12	5	24	229	16
ASFS X4116	221+ 4 +14	15/16	3	4	-	9	4+6+11	5	20	188	14
ASFS X4117	221+ 3 +11	16/16	3	6	-	7	4+6+13	5	22	194	14
ASFS X4118	228+ 4 +14	16/18	3	4	-	9	3+6+12	4	23	215	16
ASFS X4119	222+3/4+13	16/17	3	4	-	9	4+6+12	4	25		
ASFS X4120	214+ 4 +11	16/17	3	4	-	9	4+8+10	4	22	181	12
ASFS X4121	225+ 4 +14	16/18	3	4	-	8	4+6+11	5	26	227	16
ASFS X4122	226+ 4 +14	15/16	3	4	-	7	4+6+11	5	21	187	14
ASFS X4123	222+ 3 +13	15/17	3	4	-	7	4+6+11	4	19	131	7
ASFS X4124	222+ 3 +13	16/16	3	4	-	8	4+6+12	4	19	126	8
ASFS X4125	226+ 3 +14	16/18	3	4	-	9	4+6+12	5	18	113	8
ASFS X7381	225+ 4 +14	16/18	3	4	-	7	4+6+11	6	24	224	15
ASFS X7382	227+3/4+12	16/18	3	4	-	9	4+6+10	4	23	211	14
ASFS X7383	221+ 3 +14	16/18	3	4	-	9	4+8+10	5	25	222	16
ASFS X7384	229+ 3 +12	15/16	3	4	-	9	4+6+13	5	23	209	15
ASFS X7385	224+ 3 +13	16/18	3	4	-	7	4+6+11	5	22	215	13
ASFS X7386	224+ 3 +14	16/18	3	4	-	7	4+6+10	5	23	210	14
ASFS X7387	220+3/4+13*	16/18	3	4	-	9	4+6+13	6	25	214	13*
ASFS X7388	227+ 3 +14	15/18	3	4	-	9	4+7+10	5	21	195	14
ASFS X7389	224+ 4 +12	16/16	3	4	-	9	4+8+12	5	21	183	12

ASFS X7390	226+ 3 +13	15/18	3	3	-	8	4+6+12	6	23	194	13
ASFS X7391	227+3/4+13	16/19	3	4	-	9	4+6+12	3	22	189	14
ASFS X7392	227+ 4 +14	16/18	3	4	-	8	4+6+12	6	21	194	14
ASFS X7393	225+ 4 +13	17/18	3	4	-	8	4+6+12	4	22	182	13
ASFS X7394	222+ 3 +14	16/18	3	4	-	9	4+6+11	6	22	190	14
ASFS X7395	229+ 3 +13	16/18	3	4	-	9	4+6+12	4	22	190	13
ASFS X7396	227+ 3 +14	16/17	3	4	-	9	4+8+13	3	17	106	6
ASFS X7397	224+ 4 +14	16/18	3	4	-	9	4+6+11	3	18		
ASFS X7398	226+4/3+14	16/16	3	4	-	8	4+6+11	3	16	102	7
ASFS V4798	219+ 3 +15	16/16	3	4	-	9	4+9+13	3	16	238	19
ASFS V4802	232+4/2+15	16/18	3	4	-	9	4+8+13	5	24	230	16
ASFS V5081	228+ 3 +13	17/19	3	4	-	8	4+8+12	7	25	227	15
ASFS X7433	233+ 3 +14	16/18	3	4	-	8	4+6+11	7	26	226	14
ASFS X7434	229+ 3 +15	16/16	3	4	-	9	4+8+11	6	27	240	16
ASFS V6168	236+ 3 +15	14/18	3	4	-	8	4+8+12	4	19	183	13
A. XERA											
UPR 84a	224+ 4 +13	16/16	4	2	5	-	4+6+10	8	25	236	16
UPR 84b	221+2/3+14	14/16	3	1	4	-	4+8+10	10	32	181	14
UPR 86	224+2/3+13	14/16	3	4	5	-	4+8+11	8	24	245	18
UPR 91	234+ 3 +16	14/14	3	4	-	-		7	22	241	18
ASFS V6408	221+ 3 +13	14/14	2	2	4	-	4+6+12	7	17	168	10
ASFS V6418	220+ 3 +13	14/16	3	4	-	-	4+8+12	7	16	140	9
ASFS V6423	220+ 2 +13	14/16	4	5	-	-	4+6+13	6	18	162	11
ASFS V6427	233+ 2 +15	14/16	2	4	5	-	4+7+11	6	19	202	14
UMMZ 73844	226+ 3 +14	13/15	3	4	-	-	4+6+12	7	22	237	20
UIMNH 56910	225+3/4+10	14/16	3	2	4	-	4+6+10	7	18	193	11
ASFS V5646	234+ 2 +13	14/16	3	3	4	-	4+6+8	7	17	186	12
USNM 152588	231+ 2 +14	14/16	3	4	-	-	4+6+10	6	16	170	11
ASFS V5659	225+ 3 +13	14/16	3	3	5	-	4+7+12	7	17	188	13
ASFS V5661	232+ 3 +13	14/15	3	3	4	-	4+6+10	7	17	191	12
MCZ 81019	232+ 2 +13	14/16	3	1	4	-	4+6+12	7	19	210	13
ASFS V5722	226+ 3 +13	14/16	3	4	5	-	4+6+10	8	18	190	14
ASFS V5723	231+ 2 +13	14/14	3	1	4	-	4+6+10	7	18	195	12
AMNH 94170	229+ 3 +14	14/16	2	4	4	-	4+6+10	7	16	158	12
ASFS V6616	233+ 2 +13	14/15	3	2	5	-	4+7+10	8	17	194	13
ASFS V6617	224+ 3 +14	13/15	3	2	5	-	4+8+12	7	17	175	12
ASFS V6618	228+ 3 +13	14/16	3	5	-	-	4+8+11	9	17	185	12
ASFS V6619	227+ 2 +13	14/15	3	4	-	-	4+8+12	9	17	177	12
ASFS V6636	231+ 2 +14	14/14	3	5	-	-	4+8+11	8	17	186	12
ASFS V6637	237+ 3 +14	14/14	3	4	9	-	4+8+13	7	16	187	14
ASFS V6638	234+ 2 +13	12/14	3	2	4	-	4+7+11	9	17	178	11
ASFS V6639	232+ 2 +14	14/14	3	5	-	-	4+6+11	7	17	170	11
ASFS V6640	229+2/3+13	14/15	3	4	-	-	4+8+10	7	15	162	11
ASFS V6646	230+ 2 +14	13/14	3	1	4	-	4+8+11	8	17	203	14
ASFS V6647	228+3/2+14	14/14	3	4	-	-	4+7+13	8	18	192	13
ASFS V6648	228+3/4+12	14/16	3	2	5	-	4+8+11	8	17	200	13
ASFS V6649	228+2/3+15	14/16	3	3	4	-	4+7+10	7	16	193	13
ASFS V6650	229+ 3 +13	14/14	3	3	4	-	4+8+11	8	16	191	13
ASFS V6651	234+ 3 +14	14/15	3	3	5	-	4+7+10	8	16	187	12
ASFS V6652	223+ 3 +13	14/14	3	4	-	-	4+8+10	9	17	187	13
ASFS V6653	225+ 2 +14	13/14	3	4	-	-	4+8+10	8	16	183	12
ASFS V6654	227+ 3 +13	14/16	3	2	5	-	4+8+10	7	17	186	13
ASFS V6655	229+ 3 +13	14/14	3	4	-	-	4+8+10	8	17	181	12
ASFS V6656	225+ 2 +14	14/16	3	1	3	-	4+8+11	8	17	181	12
ASFS V6657	230+ 2 +15	14/14	3	2	5	-	4+8+11	7	15	139	9
CM 40577	228+ 3 +14	14/14	3	5	-	-	4+8+9	9	17	196	14
CM 40578	225+ 2 +5*	14/15	3	3	5	-	2+8+10	7	17	180	4*
RT 1333	227+ 3 +12	14/14	3	4	-	-	4+7+11	8	16	181	11
RT 1334	228+ 2 +14	13/14	3	4	-	-	4+8+10	8	17	191	14
ASFS V6587	231+ 3 +14	14/15	3	2	5	-	4+6+12	8	18	221	15
UMMZ 73846	235+ 3 +15	14/16	3	5	-	-	4+6+11	7	16	147	11
ASFS V5800	231+ 3 +14	14/16	3	3	6	-	4+8+12	8	16	191	13
MCZ 36301	230+ 4 +13	14/14	3	4	-	-	4+7+12	7	18	189	14

A. SCHMIDTI

ASFS V5432	200+ 3 +19	14/16	2	3	- 7	4+6+12	192 19
ASFS V5433	201+ 3 +20	13/16	2	4	- 7	4+5+8	182 17
ASFS V5434	199+ 3 +18	14/16	2	3	- 6	4+6+13	189 19
ASFS V5435	200+ 3 +20	13/16	2	3	- 7	4+8+10	176 17
ASFS V5436	200+ 3 +20	13/16	2	3	- 6	4+6+12	159 17
ASFS V5437	196+ 3 +8*	14/16	2	3	- 7	4+6+11	138 7*
ASFS V5334	199+ 3 +21	14/16	3	4	- 7	4+6+11	119 12
ASFS V5197	200+ 3 +22	14/16	2	4	- 7	4+8+10	224 26
ASFS V5198	196+ 3 +20	14/16	2	3	- 6	4+6+11	201 23
ASFS V5199	201+ 3 +20	14/16	2	4	- 6	4+8+10	180 20
ASFS V5258	202+ 3 +21	14/16	2	3	- 6	4+6+11	221 23
ASFS V5259	202+ 3 +21	14/16	2	4	- 7	4+8+8	208 24
ASFS V5260	204+ 3 +21	14/16	2	2	- 6	4+6+11	105 11
ASFS V5268	200+3/4+20	16/17	3	4	- 6	4+6+11	123 13
ASFS V5910	197+ 2 +8*	14/16	2	4	- 7	4+6+11	195 11*
ASFS V5923	205+3/2+21	14/16	2	4	- 7	4+8+9	194 21
ASFS V5924	207+ 3 +21	14/16	2	4	- 6	4+8+10	183 19
ASFS V5871	201+ 4 +21	14/16	2	5	- 7	4+8+14	240 26
ASFS V5999	200+ 3 +21	14/18	2	2	- 6	4+6+10	212 24
ASFS V6028	201+ 3 +21	14/17	2	4	- 6	4+7+9	220 24
ASFS V6029	192+ 3 +20	14/16	2	4	- 7	4+6+12	200 22
ASFS V5959	196+3/2+20	14/17	2	3	- 6	4+6+11	137 14
ASFS V5940	195+ 3 +7*	14/16	2	1	- 6	5+6+12	200 11*

A. FENESTRATA

ASFS V7504	243+ 2 +13	14/16	3	4	- 10	4+6+10	238 15
ASFS V7505	250+ 2 +13	14/16	3	4	- 9	4+6+10	166 11
ASFS V7564	243+ 2 +12	14/16	3	4	- 10	4+6+8	208 11
ASFS V8066	248+ 2 +12	14/15	3	4	- 10	4+6+9	252 14
VINP 1478	247+ 2 +13	14/16				4+6+9	250 17
VINP 1479	243+3/2+13	14/16				4+6+10	251 18
VINP 1485	246+ 2 +13	13/14				4+6+11	237 15
VINP 1490	246+3/2+13	14/16				4+6+10	232 16
VINP 1496	251+ 2 +12	14/14				4+6+11	262 16
VINP 1497	241+2/3+12	14/17				4+6+9	232 16
ASFS V7921	247+ 2 +14	14/14	3	4	- 9	4+7+8	148 10
ASFS V7940	248+ 2 +13	14/14	3	4	- 9	4+7+10	230 13
ASFS V7984	243+ 3 +14	14/15	3	4	- 8	4+6+9	228 13
ASFS V7985	248+ 2 +14	14/16	3	4	- 9	4+6+10	226 14
RT 977	242+ 2 +14	14/15	3	4	- 9	4+6+11	155 11
ASFS V3805	240+ 2 +12	15/17	3	4	- 9	4+6+9	257 15
ASFS V3806	245+ 3 +13	15/16	3	4	- 9	4+6+9	225 14

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THE BRAIN OF THE EMU *DROMAEUS NOVAEHOLLANDIAE*

II. ANATOMY OF THE PRINCIPAL NERVE CELL GANGLIA AND TRACTS[1]

BY STANLEY COBB

INTRODUCTION

This contribution is to supplement a paper published recently (Cobb and Edinger, 1962) on the gross anatomy of the brain and pineal body of the emu. Microscopic serial sections[1] were made of the whole of one of these brains (#104), embedded in celloidin, and cut at 25 microns thickness. The sections were stained with cresyl violet for cell bodies and with Loyez modification and Weigert's stain for myelinated nerve fibers. Pieces of the other brain (#85) were cut for Golgi and Bielschowski stains, for axons and glia. The report here presented, however, is far from being a thorough description of the histology of the emu's brain; it is a description of the large neuronal divisions, the gray masses of nerve cells, and the conspicuous fiber tracts. This is to enable the reader to obtain a general picture of the distribution of the gray matter in ganglia, nuclei, and cortex, the relation of the main ganglia to each other, and their main connections by tracts. Such a picture may serve as a basis for comparing the general neuronal arrangement of the emu's brain with other avian brains. An attempt has been made to estimate the size of different ganglia, but because of shrinkage in fixation and embedding, the absolute volumes are difficult to measure. A comparison of the size of one ganglion to another in the same brain, however, is possible with reasonable accuracy. Such measurements have significance in relation to function (Cobb, 1964).

[1] From the Museum of Comparative Zoology, and the Department of Neurology and Psychiatry, Harvard University, and the Laboratory for Psychiatric Research, Massachusetts General Hospital.

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I wish to thank Dr. Paul I. Yakovlev for his help in preparing the serial sections and in photographing and naming the various structures shown.

THE CEREBRAL VENTRICLES

In order to understand the brain of any bird, one must get an understanding of how the ventricular spaces are arranged, because they have a special relation to the cortex and corticoid areas. The ventricles of the avian brain are unlike those of other vertebrates, and among birds vary in shape and size. The ventricular system is filled with fluid and extends from the olfactory bulb to the spinal cord. In much of its course it is narrow; in the cerebral hemispheres it is often only a potential space, moistening two layers of brain which lie one upon the other (see Fig. 9).

In the olfactory bulbs the size of the ventricle varies greatly, from a tiny ependymal slit in the single fused bulb of small passerine birds, such as *Passer* (house sparrow), to a large open chamber in *Diomedea* (albatross) which has big separate bulbs. In the emu the ventricle is distinct but not large (Figs. 2, 3). The ventricle of the olfactory bulb is directly connected with the lateral ventricle of the cerebral hemisphere. This lateral ventricle lies between septum and striatum with its long dimension vertical (Figs. 4, 7). As it spreads backward it becomes larger, and as the mid-sections of the brain are reached the ventricle is seen to extend more and more laterally over the striatum (Figs. 8, 9). Here it lies under a sheet of tissue composed anteriorly of dorsal hippocampus and parahippocampus (Fig. 7), and farther back of corticoid tissue of three kinds: parahippocampal, dorsolateral and periamygdalar (Figs. 8, 10). Thus, over approximately the caudal third of the emu's cerebral hemispheres, the ventricle is a narrow, potential space separating a sheet of supraventricular tissue from the main mass of the underlying ganglia. The relation to the *nucleus diffusus*, or wulst (Fig. 4) is important. In the emu the wulst is frontally placed so the ventricles remain largely medial and vertical until the wulst becomes smaller caudally and the vallecula flattens out (Figs. 4, 5). Farther back, the ventricle spreads widely to each side and around to the base, making a complete covering of the occipital pole of the hemisphere (Figs. 9, 10).

The two lateral ventricles join at the base of the hemisphere, forming the third ventricle. This is continuous with the single ventricular space of the midbrain (aqueduct) which is large with lateral out-pocketings into the big optic lobes (Fig. 11). Much of these lateral ventricles of the midbrain appears to be

merely potential spaces, but at their mesial portions, where they join the aqueduct, the lumen is distinctly patent. Below the level of the midbrain the fourth ventricle is seen, wide beneath the cerebellum and narrowing down to become covered with nervous tissue in the medulla near the spinal cord.

ANATOMY OF THE FOREBRAIN

In birds, the main mass of the forebrain is composed of large gray ganglia (the "striatum") with a relatively small corticoid part, and variable, but usually small olfactory bulbs. Strictly speaking, the striatum of higher mammals is composed of the more dorsal cerebral gray ganglia traversed by bands of white fibers. Many of these run to and from the neocortex, making the striped appearance that gave the area its name. Such a combination of gray and white matter develops of necessity wherever there are gray ganglia forming axonal connections with each other. The naming of these ganglia in mammals and birds, as if they were homologous structures, has led to no little misunderstanding (Table 1). Rose (1914) was wise enough to simply name his ganglia A, B, C, etc., and Kuhlenbeck (1938), relying on embryological evidence, developed a nomenclature for the cerebral ganglia of birds that largely disregarded mammalian analogies. His work has been substantiated and effectively used by Jones and Levi-Montalcini (1958). Kuhlenbeck's investigations show that the ganglia (he calls them "nuclei") of the avian cerebral hemisphere arise from four embryonic zones, dorsomedial and ventromedial (the larger olfactory part) and dorsolateral and ventrolateral (the striatal nuclei); the latter two form the main masses of the cerebral hemisphere. A conspicuous boundary, the lamina medullaris dorsalis (Fig. 6) separates the striatal nuclei into two divisions, the epibasal nuclei and the basal. This seems to be a basis for a more rational nomenclature than the one built up by Kappers *et al.* (1936) on the comparative neurology of living reptiles and birds. This nomenclature is, therefore, used in this paper in describing the forebrain. Karten and Hodos (1966) in their recent atlas of the pigeon's brain use a modified Kappers nomenclature with abbreviations, as shown in my Table I. In mentioning different parts of the striatum, I use Kuhlenbeck's names and put Karten and Hodos' abbreviations in parentheses; for example: nucleus epibasalis caudalis (A) is the archistriatum. (See Table I and Fig. 1, and the list of abbreviations.)

Table I

Comparison of Different Nomenclatures of Avian Forebrain Ganglia

COBB this paper	KARTEN and HODOS 1966	ROSE 1914	HUBER and CROSBY 1929	KUHLENBECK 1938; JONES and LEVI-MONTALCINI 1958
n. intercalatus	HIS	A	n. intercalatus hyperstriaticus	n. epibasalis dorsalis pars superior
n. diffusus	HA	B	Hyperstriatum accessorium	n. diffusus dorsalis
n. diffusus*	HD	C	Hyperstriatum dorsale	n. epibasalis dorsalis pars superior
n. epibasalis dorsalis	HV	D	Hyperstriatum ventrale	n. epibasalis dorsalis pars inferior
n. epibasalis centralis	N E	G S	Neostriatum Ectostriatum	n. epibasalis centralis
n. epibasalis caudalis	A	K	Archistriatum	n. epibasalis caudalis
n. basalis	PA	H	Paleostriatum augmentum	n. basalis
n. entopeduncularis	PP	J	Paleostriatum primitivum	n. entopeduncularis

* These three nuclei make up the wulst. In emu the *lamina frontalis* is not clearly divided into *suprema and superior* with a "hyperstriatum dorsale" lying between. The nucleus intercalatus is not well defined and lies between the fibers of the lamina in a lateral position (see Fig. 4). Therefore, in describing emu the *n. diffusus* is not subdivided but is considered to be all the grey matter lying above or within the lamina frontalis.

Figure 1 is drawn from a reconstruction of the forebrain of the emu, the main ganglia or nuclei being shown in seven sections at the levels indicated by the vertical lines drawn on the lateral view of the whole brain (insert). The wulst or nucleus diffusus (HA, HD) is seen in five sections; beginning with the most anterior it is the largest; in the second and third it is large and then tapers off in the fourth and fifth. The largest nucleus of all, the nucleus epibasalis centralis (N and E), appears as a small part of the third section and enlarges caudally until it is the only ganglion present in the most caudal section. Other main nuclei can be similarly traced to show their anteroposterior relationships. The relation of one nucleus to another in any one section can be seen in the photographic reproduction

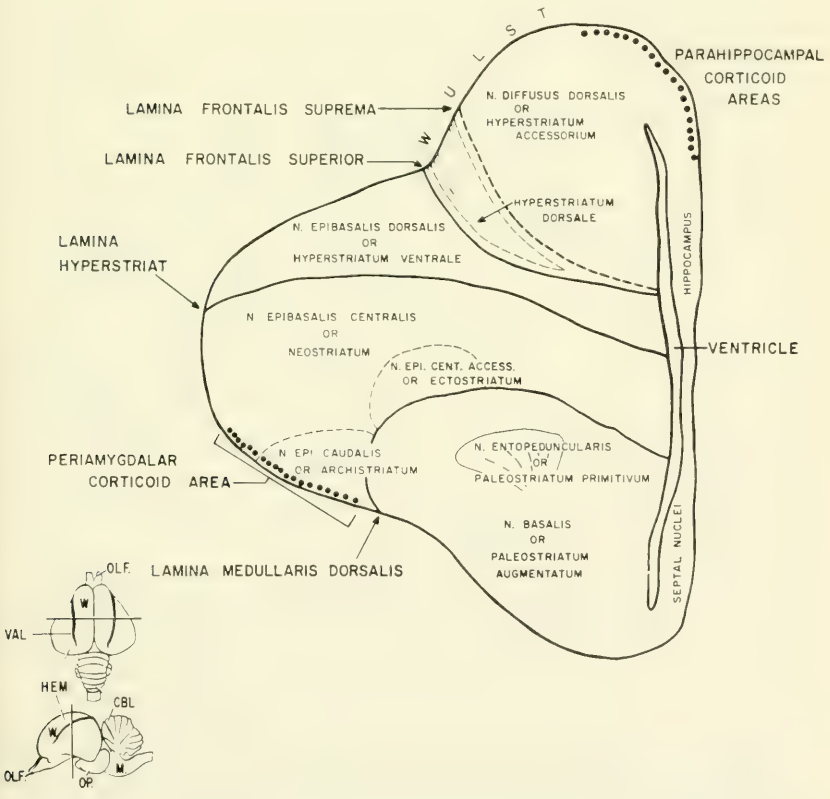

Fig. 1A. A diagrammatic representation of the dorsoventral relations of the principal forebrain ganglia, but no one section could show all of these.

of the sections that represent various levels (Figs. 2 to 11). The nucleus intercalatus is found in most birds. In the emu it is a rather inconspicuous part of the wulst lying between the fibers of the lamina frontalis (Fig. 4). It is composed of small nerve cells and is more compact than the rest of the nucleus diffusus of which it is a part (if the nucleus diffusus is defined, as in this paper, as that part of the gray mass lying within or above the lamina frontalis).

The division between wulst (nucleus diffusus) (HA, HD) and nucleus epibasalis dorsalis (HV) is quite clear in the emu, the lamina frontalis being well developed, but in my specimen it is not split into two parts, superior and suprema. Therefore, one cannot make out a distinct nucleus lying between the parts

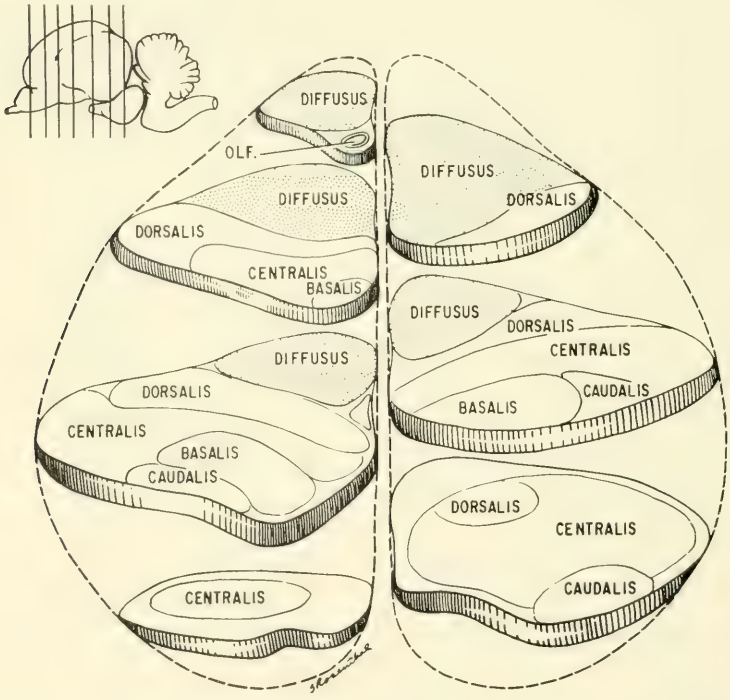

Fig. 1B. A simplified diagram of the principal forebrain ganglia showing perspective, to give some idea of the anteroposterior relationships. The serial sections from which the diagrams were drawn are (from front to back) #161, #361, #501, #701, #901, #1201, #1281. Their position on the whole brain is shown by vertical lines on the small inset.

of the lamina as described in some birds' brains. Rather, one sees a branching of the lamina frontalis with many cells lying in the interstices. Some of these are small and might be said to form a group which could be called nucleus intercalatus (Figs. 6, 7). This is not clear in sections farther forward (Fig. 4). In fact, no boundaries would seem to be definite enough to justify describing a distinct nucleus; in short, I do not find in emu a nucleus epibasalis dorsalis, pars superior (HD). Below the lamina frontalis the nucleus epibasalis dorsalis (HV) is well defined and bounded ventrally by the lamina hyperstriatica (Figs. 4, 6).

CORTEX AND CORTICOID AREAS

The question of the avian cerebral cortex (pallium) is complex and controversial. Craigie meticulously described the corticoid areas of the emu (1935 A, B). In the next year Kappers, Huber and Crosby (1936) modified Craigie's findings to some extent. Bŭres, Fifkova and Marsala (1960) have made a good summary of the "cortex question," but, unfortunately, their nomenclature differs from others. I am using the names of corticoid areas and hippocampus as used by Kappers, Huber and Crosby (1936) because they seem simpler and freer from implied homologies to mammalian brains.

In the emu there is a well developed archicortex, the hippocampus, with three or four obvious layers. These become less distinct in the dorsal hippocampus (Fig. 7), and lamination cannot be seen clearly at all in the parahippocampal corticoid areas which have a thin single or sometimes double layer of cells lying over the surface of the wulst. Further laterally, the dorsolateral corticoid area is even thinner and less distinct (Fig. 8). As one goes towards the posteroventral part of the hemisphere, a definite corticoid area with two layers of cells is seen over the nucleus epibasalis caudalis (A). This is called the periamygdaloid corticoid area (Fig. 8). Also ventral but far forward is seen another conspicuous corticoid area, the praepyriform. It lies about the root of the olfactory bulb where it joins the frontal pole of the hemisphere (Fig. 3).

The relationship of these corticoid areas to the cerebral cortex of mammals is not well understood. The fiber connections of the parahippocampal areas suggest a function analogous to that of neocortex in mammals, but these areas are surely not homologous

with mammalian neocortex; their homology to the "general cortex" of reptiles is more clear. The area described by Goldby and Gamble (1957) as "dorsal cortex" seems to correspond with what is called here "parahippocampal corticoid," and called "general cortex" by Kappers, Huber and Crosby (1936). A thickening found in this "dorsal cortex," which overlies the anterior dorsal part of the striatum, occupies a position in the pallium from which, *in the embryo*, cortex is seen to develop. In such a topographical sense only can this cortex be said to be homologous with mammalian neocortex.

There is better evidence that the periamygdalar corticoid areas are homologous with the temporal mesocortex of mammals, and that the praepyriform corticoid areas are homologous with the entorhinal areas of mammals. One thing seems sure, and that is that birds (including the emu) have no neocortex. For a scholarly and thorough discussion of this vexing question, the reader is referred to Kuhlenbeck's recent book (1966).

COMPARATIVE MEASUREMENTS OF GANGLIA IN THE FOREBRAIN

Believing that increase of any function in an animal is positively correlated with increase in size of the parts of the brain significantly involved, it is of interest to compare the sizes of the different parts of the brains of birds of various families and varied types of behavior. This has been done in relation to the auditory nuclei (Winter, 1963), the olfactory bulbs (Cobb, 1960), auditory and visual centers of the midbrain (Cobb, 1964), and ganglia of the forebrain (Fritz, 1949). Since we know so little about the function of the different ganglia of the forebrain, it is difficult to choose which ganglia to measure. Fritz showed differences in size of the ganglia he measured, but no correlations with any functions. He chose to measure the volume of "hyperstriatum" (n. diffusus plus n. epibasalis dorsalis), "neostriatum" (n. epibasalis centralis), "archistriatum" (n. epibasalis caudalis), and "paleostriatum" (n. basalis plus n. entopeduncularis). The boundary between the neostriatum and archistriatum is not always clear, as pointed out by Fritz.

I decided to measure: 1) n. diffusus, both parts plus n. intercalatus (i.e. all the ganglionic mass above the lamina frontalis superior); 2) the n. epibasalis dorsalis (HV); 3) the n. epibasalis centralis (N, E). The first was chosen because it seemed, grossly, to vary so much from species to species, the

other two because they are large forebrain ganglia and are possibly associative in function and hence related to "higher integrations" and "intelligent" behavior (Table II).

In the brainstem the n. isthmi, n. mesencephalicus, and tectum opticum were chosen because of their relation to hearing and vision, as described in a previous paper (Cobb, 1964), and by Karten (1966). The method of estimating the volume of each of these ganglia and of the whole hemisphere, with which they are compared, has been described previously (Cobb, 1964). Briefly, it is to project and draw the structures to scale, and, by knowing the thickness of the sections and their distances apart and number, to compute the volume. Absolute values for volumes of different structures are not reliable because of differences in shrinkage from one brain to another, but relative measurements in any one series of slides made from one brain are significant.

An attempt was made to measure the areas of the hippocampus and the corticoid structures, but because of their long and narrow shapes, it was difficult to use the planimeter to measure their areas. Photographs were therefore made to scale and the desired areas were cut out of each print and weighed. By this method (Fritz, 1949), it was estimated that the n. diffusus (HA and HD) had a volume 28 per cent as large as the hemisphere, and that the hippocampus plus the corticoid areas had a volume 13 per cent of the size of the hemisphere. By the projection planimeter method (Cobb, 1964) the n. diffusus (HA and HD) was also found to be 28 per cent of the hemisphere. For these quantitative data on the emu brain see Table II.

Table II

Volumes of Certain Parts of Emu Brain

Volume of one cerebral hemisphere (before fixation) approximately 6.3 cc	*percentage of hemisphere*
Nucleus Diffusus (HA & HD)	28
N. Epibasalis Dorsalis (HV)	11
N. Epibasalis Centralis (N & E)[1]	32

Volume of one optic lobe (before fixation) approximately 0.5 cc	*percentage of optic lobe*
N. Mesencephalicus Lateralis	5.4
N. Isthmi Magnocellularis	1.9
N. Isthmi Parvocellularis	2.5
Tectum Opticum	81.0

[1] As defined in section on abbreviations and nomenclature and Fig. 1.

As to the compactness of the emu's brain, it is obvious by microscopic inspection that there are fewer nerve cell bodies (perikarya) in a given area than in the brains of smaller birds. Comparison was made by counting the number of cells in 0.0143 of a square millimeter in microscopic slides of brain tissue of the emu and of a hummingbird (*Selasphorus platycercus*). Knowing the thickness of the section, the number of cells per cubic millimeter was computed for stratum E of the optic tectum of the midbrain, and for the midposterior part of the n. epibasalis centralis (N). In each of these cases the emu was found to have less than half as many cells per cubic millimeter as the hummingbird (see Table III). Purkinje cells in the cerebellum were also counted and measured in these two birds, and the ratio of 1 to 2 was also approximated. Because of the linear arrangement of Purkinje cells along the edge of a stratum, cells per volume could not be counted, but cells per linear micron of the layer were easily figured. One should not lay too much claim to accuracy in these determinations of cells per given volume, because in the process of fixing and embedding in celloidin, there is much shrinkage of the brain tissue, and the amount of shrinkage in two separately prepared series of brain sections cannot be accurately estimated. In my series of brains it seems to be about 20 or 23 per cent of the volume of the fresh brain. The figures are given in tabular form, with emphasis on the fact that they are only approximate (Table III).

Table III

Estimates of Compactness of Emu Brain Compared to Hummingbird

	Dromaeus novaehollandiae	*Selasphorus platycercus*
Number of cells per mm^3 of n. epibasalis centralis (N).	42,800	125,000
Number of cells per mm^3 of stratum E of tectum	40,000	100,000
Purkinje cells per 100 linear micra	2.2	4.8
Average diameter of Purkinje cells	26.0 micra	12.0 micra

GRAY NUCLEI AND LAMINAE OF MIDBRAIN AND HINDBRAIN

Figures 8 to 12 show the main gray masses of the midbrain and hindbrain; these masses are either nuclei, large and small, or laminated structures such as the nerve cell layers of the tectum opticum and cerebellum. This laminate pattern has neurons oriented in three planes, the axons usually parallel and the dendrites and collaterals at right angles, making a criss-cross arrangement in which layers of cells are more or less clearly separated by layers of fibers. Such an arrangement of neurons probably is more plastic in function than the arrangement in nuclear masses, allowing more rapid and efficient adaptations to environmental change (Yakovlev, 1952). The acme of such development is seen in the mammalian cerebral neocortex. In birds, where vision is of such great importance, it is remarkable that a visual cortex has developed in the tectum of the midbrain, but none in the forebrain.

The cerebellum, in the hindbrain, is an example of an organ with laminated cortex, subserving rapid coordination in widespread neuronal integrations. The three-layered arrangement of neurons is uniform throughout the wide extent of this cortex (Fig. 12).

Sections were made of the pineal body, but were stained only with hematoxalin and eosin, so no refinements of histology could be identified. However, one could see the structures described by Quay (1965): a sac-like formation, tubules and follicles, and a mass of cellular parenchyma. In two areas there were conspicuous lymphoid nodules. In general, the histology of the pineal body is more like that of the Galliformes than the Passeriformes.

SUMMARY

The emu, like the ostrich, is an enormous running bird and cannot fly. This specimen weighed 31 kilograms. The brain of the emu is one of the largest avian brains, and less compact than the brains of smaller birds. The forebrain is well developed with medium sized hippocampus and parahippocampal corticoid areas. The size of these areas is probably related to the medium size of the olfactory bulbs. The gray nuclei that make up the forebrain are much like those of *Gallus* in arrangement and relative size, except for the nucleus diffusus (wulst or hyperstriatum

accessorium) which is relatively larger and is bounded below by a loosely arranged lamina frontalis. This cannot be divided into two parts, superior and suprema. The nucleus intercalatus is represented by a group of small cells in the lateral part of the area crossed by the sparse upper fibers of the lamina frontalis. Little is known about the function of the wulst. Its connections with the optic tectum of the midbrain indicate that it has something to do with vision, and the large size of the emu's eye suggests a reason for the big wulst.

The midbrain is remarkable for its large optic tectum with seven definite layers, but this visual cortex is conspicuous in all birds, the emu rating above the average of most birds in relative size of tectum, but not as high as the Falconidae. In the hindbrain there is nothing remarkable; the cerebellum is well developed but not relatively as large as in many birds with skill in flying.

REFERENCES

Bŭres, J., E. Fifkova and J. Marsala

1960. Leao's spread in depression in pigeons. J. Comp. Neurol., **114:**1.

Cobb, S.

1960. A note on the size of the avian olfactory bulb. Epilepsia, **1:**394-402.

1964. A comparison of the size of an auditory nucleus (n. mesencephalicus lateralis, pars dorsalis) with the size of the optic lobe in 27 species of birds. J. Comp. Neurol., **122:** 271-280.

Cobb, S. and T. Edinger

1962. The brain of the emu (*Dromaeus novachollandiae*, Lath) 1. Gross anatomy of the brain and pineal body. Breviora, Mus. Comp. Zool. No. **170:** 1-18.

Craigie, E. H.

1935a. The hippocampal and parahippocampal cortex of the emu. J. Comp. Neurol., **61:** 563.

1935b. The cerebral hemispheres of the kiwi and emu. J. Anat. **69:** 380-393.

Fritz, W.

1949. Vergleichende Studien über den Antiel von Striatumteilen am Hemisphärenvolumen des Vogelhirns. Rev. Suisse Zool., **56:** 461-491.

Goldby, F. and H. J. Gamble

1957. The reptilian cerebral hemispheres. Biol. Rev., **32:** 383-420.

Huber, C. G. and E. C. Crosby

1929. The avian diencephalon. J. Comp. Neurol., **48:** 1-177.

Jones, A. E. and R. Levi-Montalcini
1958. Patterns of differentiation of the nerve centers and fiber tracts in the avian cerebral hemispheres. Arch. Ital. Biol., **96:** 231-281.
Kappers, C. U. A., G. C. Huber and E. C. Crosby
1936. The comparative anatomy of the nervous system of vertebrates, including man. New York, MacMillan, 2 vols.
Karten, H. J. and W. Hodos
1966. Stereotaxic atlas of the pigeon's brain. (In press).
Kuhlenbeck, H.
1938. The ontogenetic development and phylogenetic significance of the cortex telencephali in the chick. J. Comp. Neurol., **69:** 273-295.
1966. Comparative anatomy of the vertebrate brain. (In press).
Quay, W. B.
1965. Histological structure and cytology of the pineal organ in birds and mammals. Progress in Brain Research, **10:** 49-86.
Rose, M.
1914. Ueber die cytoarchitektonische Gliederung des Vorderhirns der Vögel. J. Psychol. Neurol., **21:** 278-352.
Smith, G. E.
1919. A preliminary note on the morphology of the corpus striatum and the origin of the neopallium. J. Anat., **53:** 271-291.
Winter, P.
1963. Vergleichende qualitative und quantitative Untersuchungen an der Hörbahn von Vögeln. Z. Morphol. Ökol. Tiere, **52:** 365-400.
Yakovlev, P. I.
1952. Patterns of neuronal assemblies and the anatomical substratum of seizures. Epilepsia, (Ser. 3) **1:** 51-68.

ABBREVIATIONS AND NOMENCLATURE USED IN THE FIGURES

(See also Table I)

A. SEPTAL.	Area septalis
ANT. COM.	Anterior commissure, interconnects n. epi. caudales of the two hemispheres
ANT. MED. VEL.	Anterior medullary velum merges anteriorly with tectal commissure, which is the dorsal part of post. com.
CBL	Cerebellum. Its cortex has 4 layers: 1. molecular 2. Purkinje cells 3. granular 4. medullary
CENTR. GRAY	Central gray matter around ventricle

CHORIOID	Plexus chorioideus of the third ventricle
DORS. LAT. CORTICOID OR DORSOLAT. CORTICOID	Dorsolateral superficial corticoid area, anteriorly on surface of wulst, posteriorly outside the ventricle
FASC. LONG. POST.	Fasciculus longitudinalis posterior
HABENULA	An olfactory way station of epithalamus
HEM.	Cerebral hemisphere
HIPPOCAMP.	Hippocampus or cortex ammonalis
INNER GRAN.	Inner granular layer of cells.
LAM. FRONT.	Lamina frontalis. Sometimes separated into superioris and suprema
LAM. HYPERSTRIAT.	Lamina hyperstriatica
LAM. MEDUL. DORS. OR LAM. MED. DORS.	Lamina medullaris dorsalis
LAT. F. B. BUNDLE	Lateral forebrain bundle, contains tracts to thalamus, midbrain, and hindbrain
LAT. LEM.	Lateral lemniscus, lies in fibrous capsule of n. mesen. lat.
LAT. LEM., D.P.	Dorsal peduncle
LAT. LEM., V.P.	Ventral peduncle
LAT. VENT.	Lateral ventricle of the cerebral hemisphere
LAT. VENT. M.B.	Lateral out-pocketing of the midbrain ventricle beneath the tectum
M	Medulla oblongata
N. BASALIS	Paleostriatum augmentatum, the nucleus separated from neostriatum above and laterally by the lamina medullaris dorsalis; PA (Karten); Field H (Rose)
N. CEREBEL. LAT.	Nucleus cerebellaris lateralis
N. DIFF. DORS.	Nucleus diffusus dorsalis or hyperstriatum accessorium, HA (Karten), Field B (Rose)
N. DORSOLAT.	Dorsolateral nucleus of the thalamus
N. DORSOMED.	Dorsomedial nucleus of the thalamus
N. ENTOPED.	Nucleus entopeduncularis, or paleostriatum primitivum; PP (Karten); Field J (Rose)
N. EPI. CAUDALIS	Nucleus epibasalis centralis or archistriatum (amygdala); A (Karten); Field K (Rose)
N. EPI. CENTRALIS	Nucleus epibasalis centralis or neostriatum, the ganglion just below lamina hyperstriatica, N and E (Karten); Field G (Rose)
N. EPI. DORSALIS	Nucleus epibasalis dorsalis pars inferior or hyperstriatum ventrale, the ganglion lying just below the lamina frontalis; HV (Karten); Field D (Rose)
N. GENIC.	Nucleus geniculatus lateralis
N. HYPOTHAL.	Nucleus hypothalamicus

N. INTERCAL.	Nucleus intercalatus hyperstriaticus; HIS (Karten); Field A (Rose), of nucleus diffusus dorsolateralis
N. INTERPED.	Nucleus interpeduncularis
N. ISTHMI	Nucleus isthmi, pars magnocellularis
N. MESEN. LAT.	Nucleus mesencephalicus lateralis, pars dorsalis, also called torus semicircularis
N. MESEN. PROF.	Nucleus mesencephalicus profundus or tegmentopedunculopontinus
N. NERV. ABDUC.	Nucleus nervus abducentis
N. OCULOMOT.	Nucleus oculomotorius
N. OLIV. SUP.	Nucleus olivarius superior
N. OVOID.	Nucleus ovoidalis
N. PARAVENT.	Nucleus paraventricularis magnocellularis
N. PRETECT.	Nucleus pretectalis
N. ROTUNDUS	Nucleus rotundus
N. RUBER	Nucleus ruber or red nucleus
N. SPIRIFORM.	Nucleus spiriformis
N. SUBPRETECT.	Nucleus subpretectalis
N. VESTIB. LAT.	Nucleus vestibularis lateralis, Deiter's nucleus
N. VESTIB. VENTROLAT.	Nucleus vestibularis ventrolateralis
OLF.	Olfactory bulb
OLF. VENT.	Ventricle of olfactory bulb
OP.	Optic lobe
OP. CHIASM	Optic chiasm
OUTER GRAN.	Outer granular layer of cells
PARAHIP. CORTICOID	Parahippocampal corticoid areas
PERIAMYG. CORTICOID	Periamygdalar corticoid area, contiguous with the parahippocampal areas; not outside the ventricle
PONT. GRAY.	Pontine gray nuclei
POST. COM. OR P. COM.	Posterior commissure, from tectum to opposite tectum and also connects spiriform and dorsal mesencephalic nuclei
PREPYR. CORTICOID	Praepyriform corticoid area
STRAT. FIBR.	Stratum fibrosum
SUPRAOPTIC.	Dorsal supraoptic decussation
TECTUM OP.	Tectum opticum of the midbrain. Divided into six layers or strata (Huber & Crosby 1924) A. Stratum opticum B. Stratum fibrosum et griseum superficiale C. Stratum album centrale D. Stratum griseum centrale E. Stratum griseum periventriculare F. Stratum fibrosum periventriculare
TR. FRONTO-ARCHISTRIAT.	Tractus fronto-archistriaticus

TR. OCCIP.-MESEN.	Tractus occipito-mesencephalicus
TR. OP. MARG.	Tractus opticus marginalis, lamina A of the optic tectum. Input from optic nerve to tectum
TR. SEPTOMESEN.	Tractus septomesencephalicus
TR. THAL-STRIAT.	Tractus thalamo-striatalis
V. OR VAL.	Vallecula
VENT. M.B.	Midbrain ventricle or aqueduct of Sylvius
W.	Wulst

Fig. 2. Serial section #81. Olfactory bulbs, Cresyl Violet stain, magnification X 7.0.

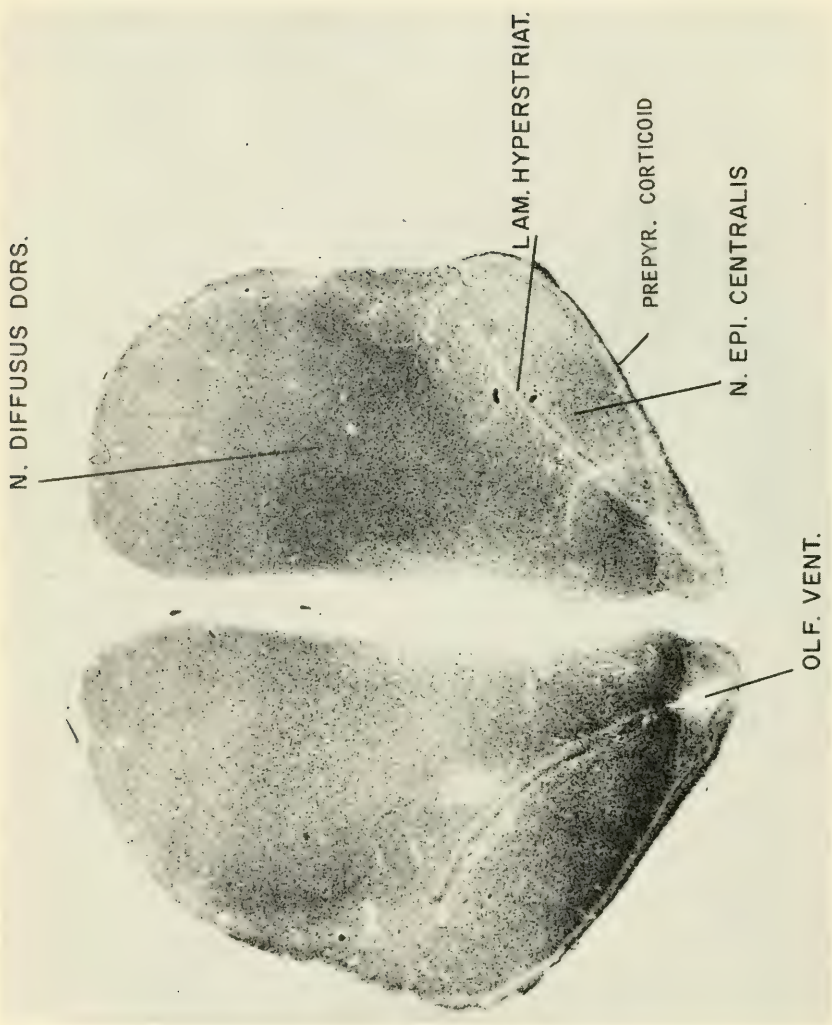

Fig. 3. Serial section #401. Cresyl Violet stain, magnification X 5.0.

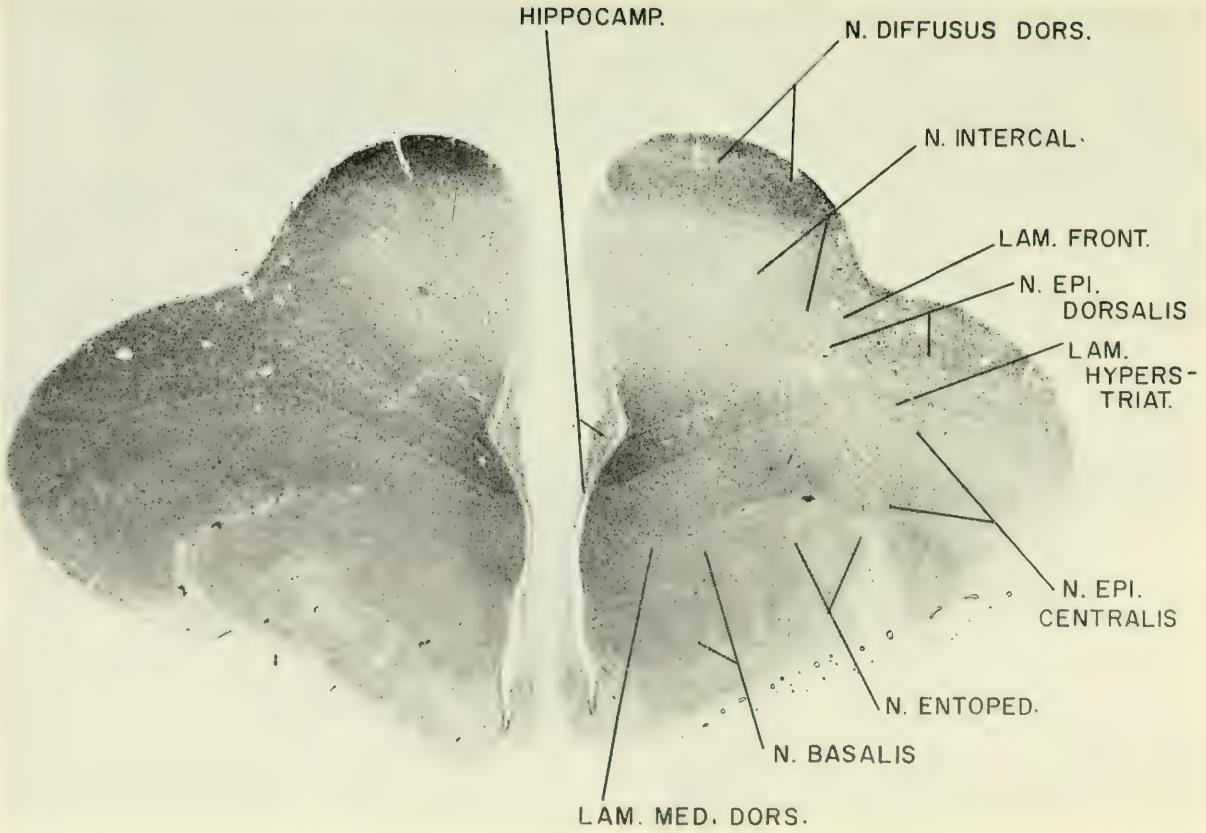

Fig. 4. Serial section #681. Cresyl Violet stain, magnification X 5.0.

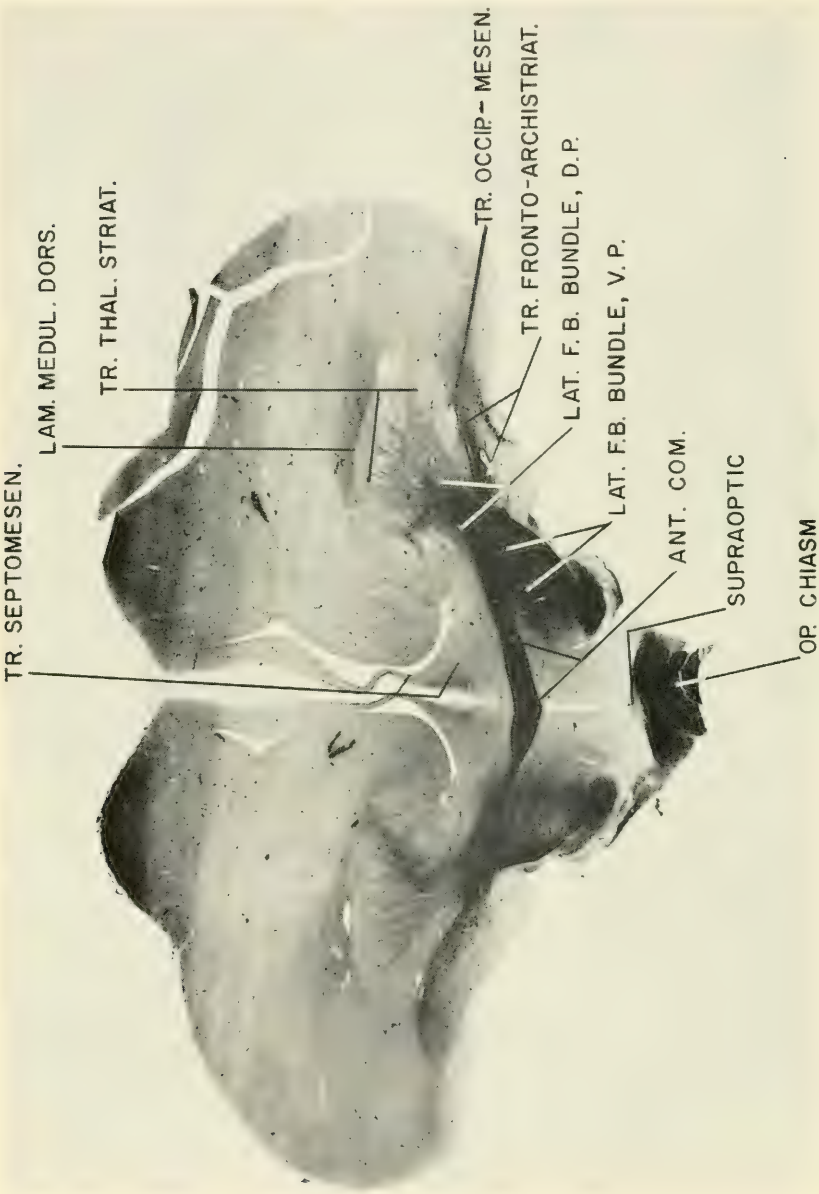

Fig. 5. Serial section #900. Loyez stain, magnification X 5.0.

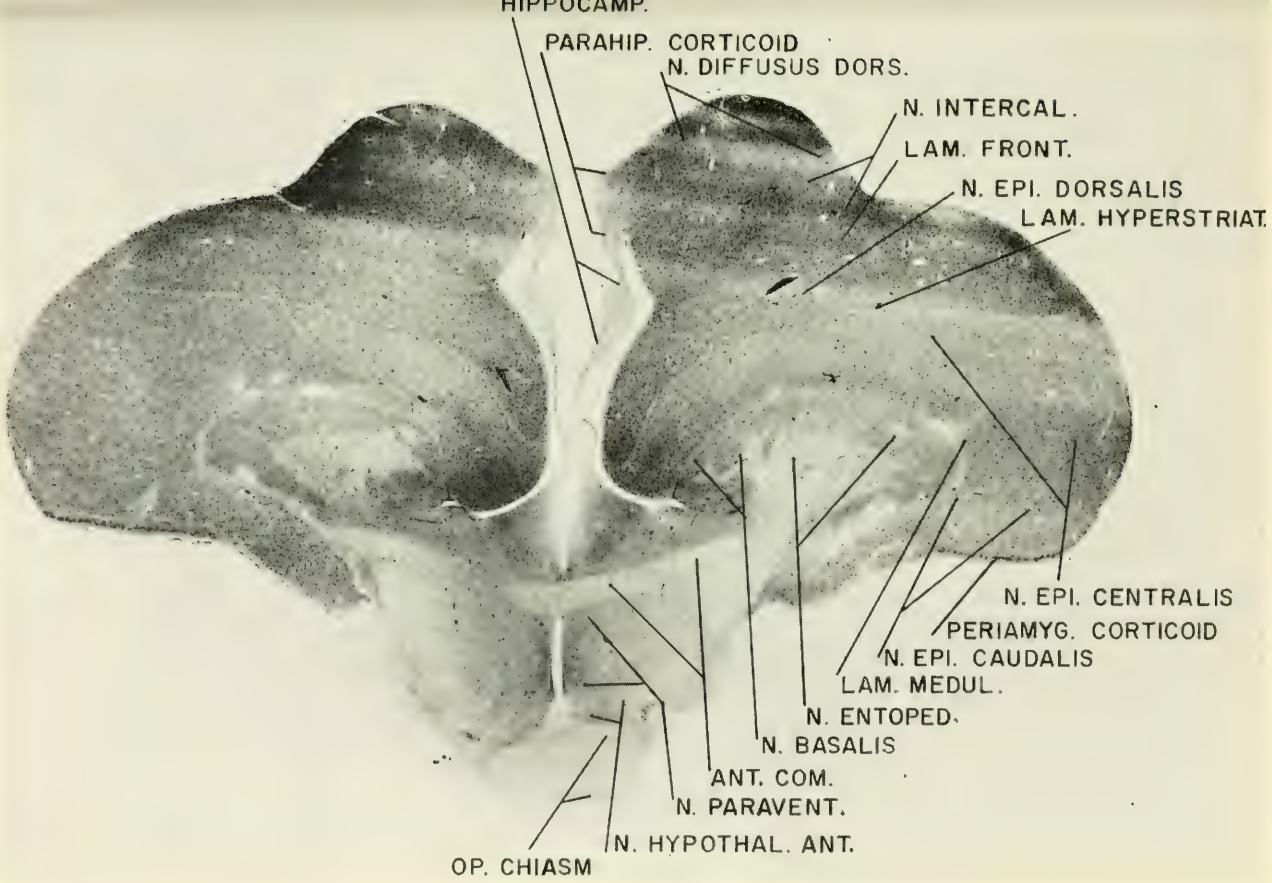

Fig. 6. Serial section #901. Cresyl Violet stain, magnification X 5.0.

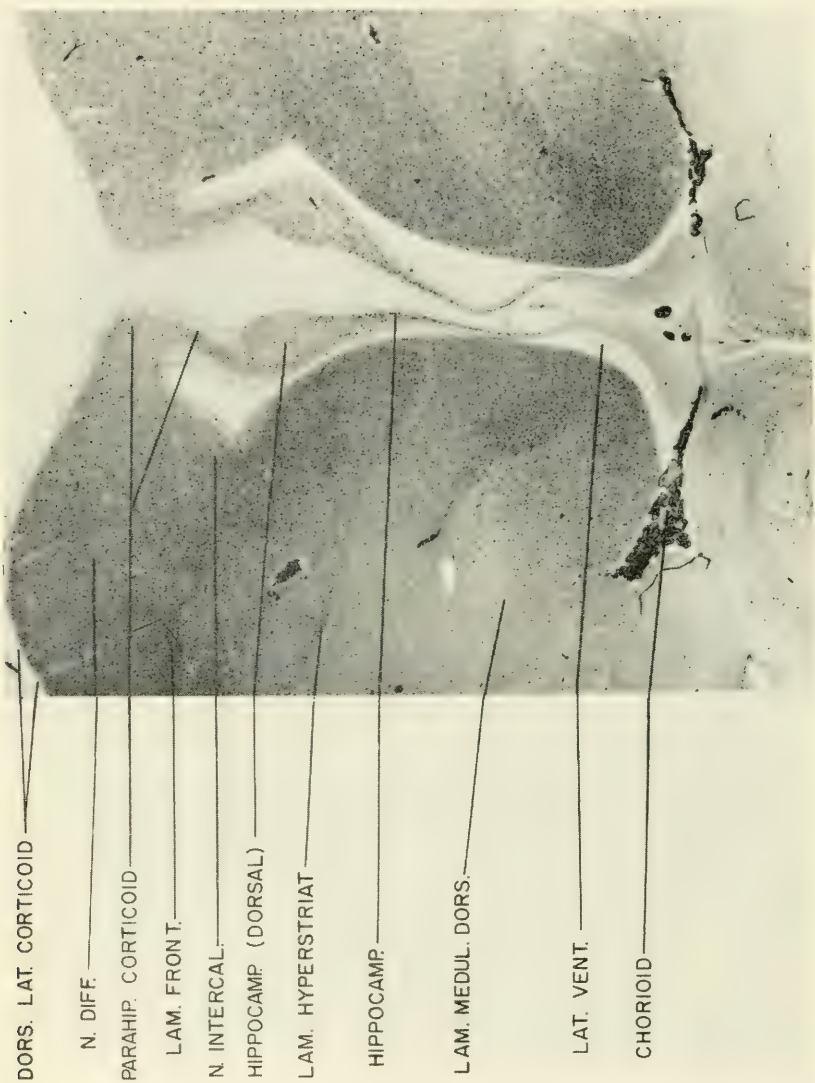

Fig. 7. Serial section #961. Cresyl Violet stain, magnification X 8.0.

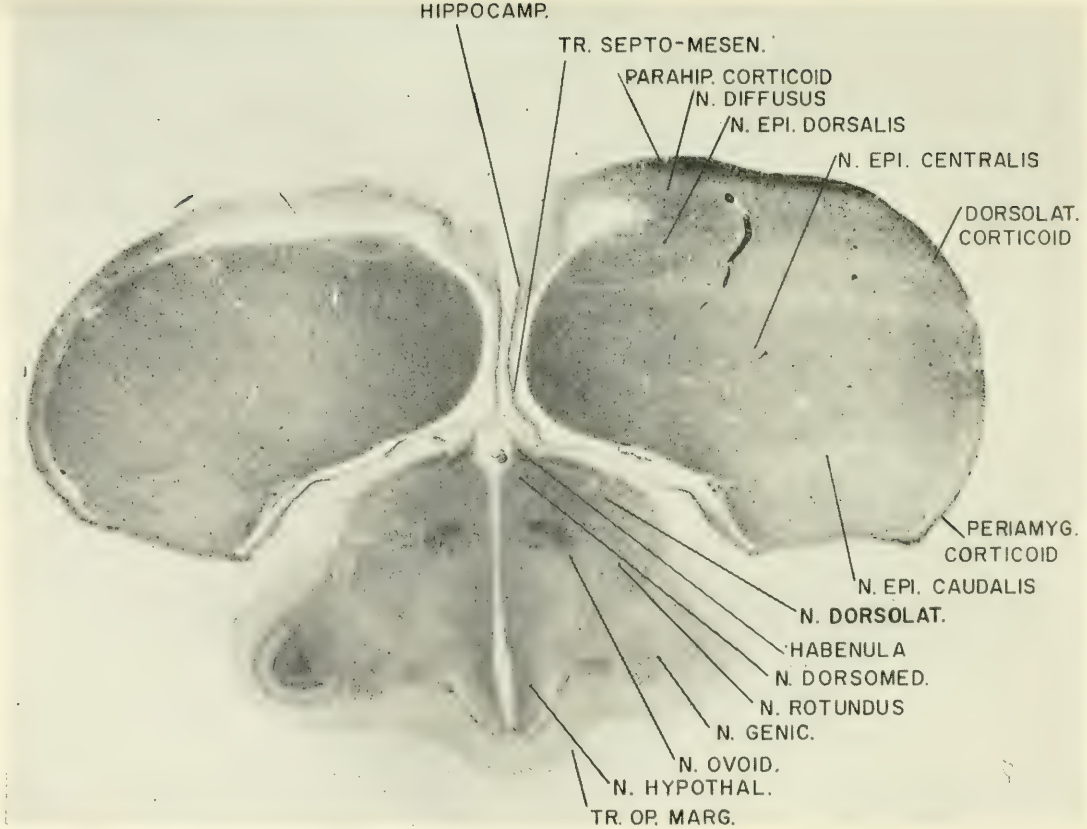

Fig. 8. Serial section #1101. Cresyl Violet stain, magnification X 5.0.

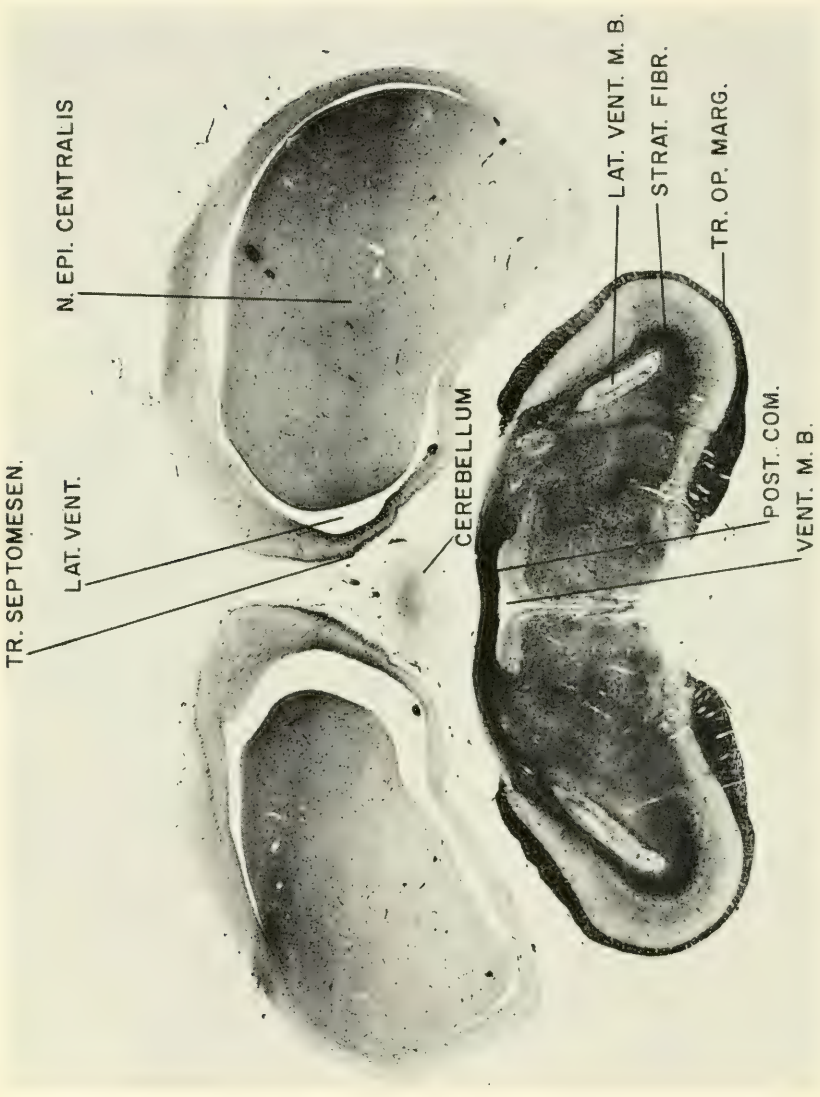

Fig. 9. Serial section #1200. Loyez stain, magnification X 5.0.

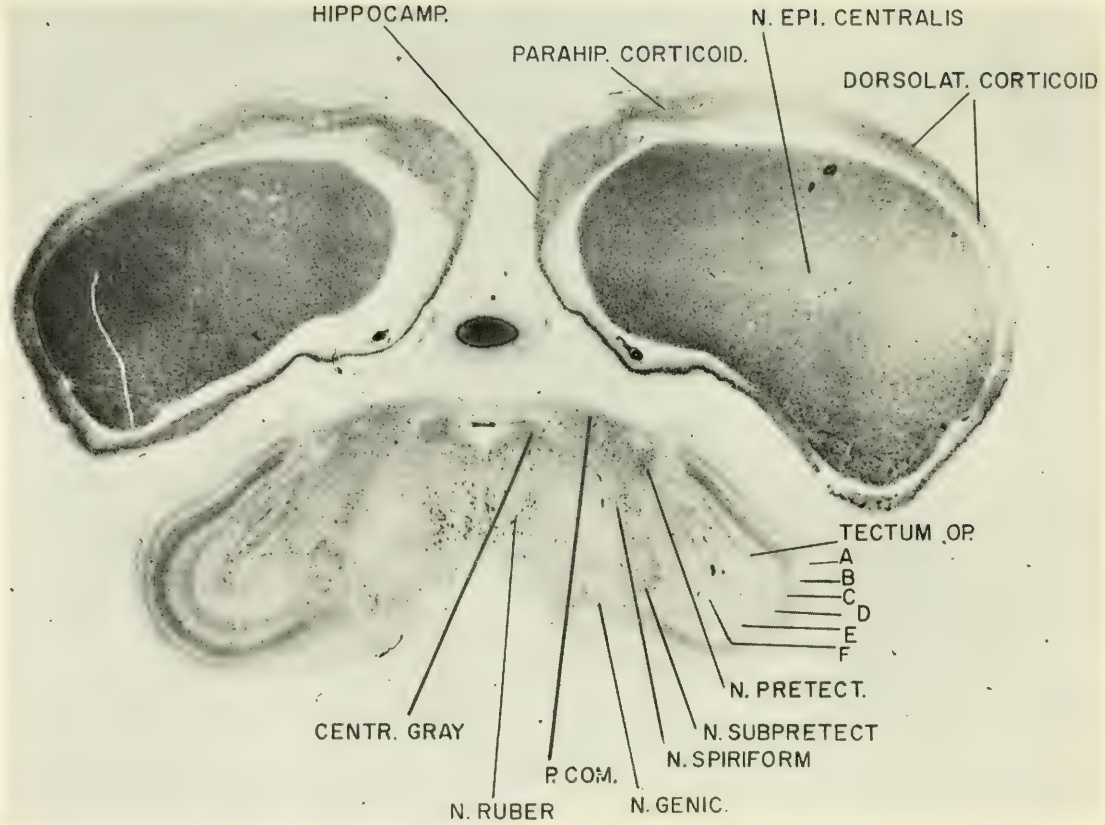

Fig. 10. Serial section #1201. Cresyl Violet stain, magnification X 5.0.

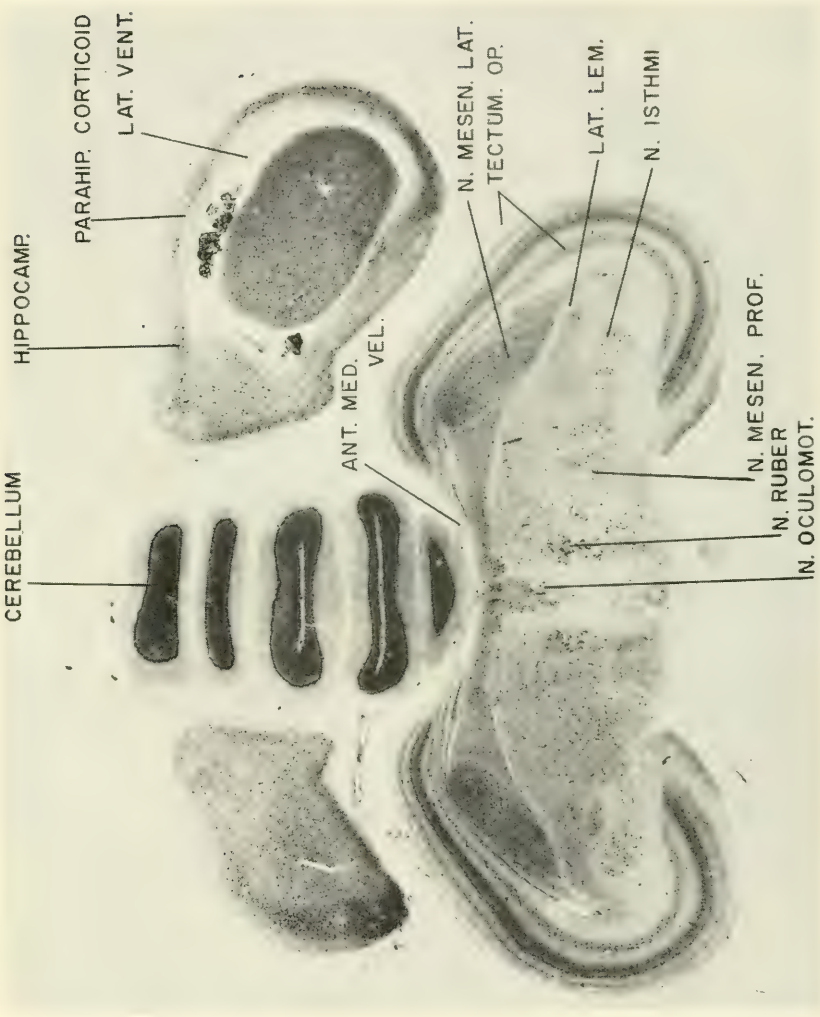

Fig. 11. Serial section #1301. Cresyl Violet stain, magnification X 5.0.

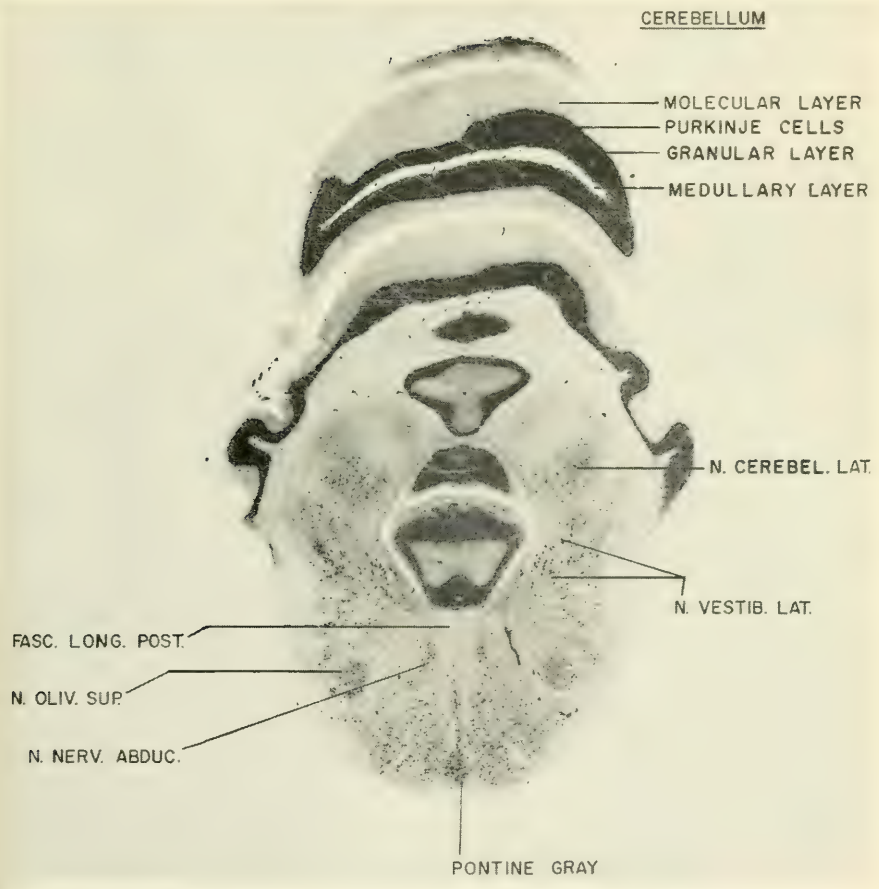

Fig. 12. Serial section #1681. Cresyl Violet stain, magnification X 5.0.

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CHRONOLOGICAL SURVEY OF THE TETRAPOD-BEARING TRIASSIC OF ARGENTINA

BY J. F. BONAPARTE[1]

SUMMARY OF PREVIOUS WORK

Ever since 1958, Argentinian paleontologists have been working intensively on continental Triassic outcrops bearing tetrapod remains, inspired by A. S. Romer's successful expedition to Mendoza and San Juan provinces in that year. The resultant collections are from both new and previously known localities; they come mainly from the Ischigualasto Formation, worked on by Romer, but also include material from a number of other formations. Exploring and collecting trips to La Rioja, San Juan, San Luis, Mendoza, and Santa Cruz provinces were made possible by many grants from the Consejo Nacional de Investigaciones Científicas y Técnicas. This support has enabled us not only to make good collections from previously known fossil-bearing localities, but also to discover new fossiliferous areas, which have broadened our view of Argentinian Triassic faunas. Materials collected in recent years include fossils from three localities in the Ischigualasto Formation, from the Los Colorados Formation of La Rioja and San Juan provinces, from the Cacheuta Formation in northern Mendoza Province, and, in addition, from a new locality in the Puesto Viejo Formation south of San Rafael, Mendoza Province, discovered by the former Dirección Nacional de Geología y Minería. A great proportion of the tetrapod material collected has been studied, and it is possible to identify the remaining material with satisfactory approximation; these studies enable us to attempt an interpretation of the chronology of some of the Argentinian Triassic formations.

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The chronology of these Triassic series has, in the past, been interpreted largely on the basis of their paleobotany, which was well summarized by Bonetti (1963). These interpretations, unfortunately, are not in complete agreement with those obtained from a study of tetrapod remains; the paleobotanic data indicate little differentiation from one formation to another, while the tetrapod data suggest clear differences, and allow a better analysis of chronology.

Bonetti's work is the most recent on the subject. She accepts the opinion of Groeber and Stipanicic, 1953, and Stipanicic, 1957, that the known Argentinian Triassic series with *Dicroidium* flora are (when present) in discordance over rocks synchronic with those known as Choiyoilitense from southern Mendoza and northern Neuquén provinces. The correlation proposed by these authors, between the Argentinian Choiyoilitense and the Porfidicqueratofiric series of the Chilean coast south of Los Vilos, is also accepted by Bonetti. She concludes that the Argentinian Triassic series with *Dicroidium* flora are essentially of Keuper age (Carnian at the lower levels, Norian at the upper). This conclusion is based on the presence of an ammonite and pelecypod fauna in sediments underlying the effusive rocks near Los Vilos, as well as on the affinities of a flora found in a lutitic level intercalated in the upper part of the Chilean effusive complex with the Argentinian Triassic flora from the Potrerillos, Cacheuta, Barreal, Cortaderita, etc., formations. In her clear and brief analysis, however, Bonetti points out the need for re-examination of the determinations of most of the marine fauna below the Los Vilos effusives. Quite apparently, the chronology of the Chilean effusive series is far from definitely clear.

In recent years some attempts at Triassic chronology have been based on tetrapod remains. Owing to the presence of *Chirotherium* footprints studied by Rusconi (1951b) and reconsidered by Peabody (1955), Stipanicic (1957) considered that the Sierra de las Higueras Formation in northern Mendoza was the oldest Triassic formation of Argentina, and referred it to the Neoscythian — Eoanisian. Romer (1960, 1962b) believes that the age of the Ischigualasto Formation is upper Middle Triassic: "surely pre-Norian and not improbably pre-Carnian." Reig (1961) considered briefly the age of four Triassic formations. He believes that the Cacheuta Formation, with both brachyopids and a proterosuchian, is more reasonably assigned to the "Eotriásico Superior" (Scythian) than to any later time. As to the age of the Sierra de las Higueras Formation as given by Stipanicic,

Reig points out the limited significance of the footprint data. As regards the Los Rastros and Ischigualasto formations, after some analysis and comparisons, he assigns an upper Ladinian age to the Ischigualasto fauna.

	Stipanicic 1957	Bonetti 1963	Reig 1961 , 1963	Romer 1960 , 1962
NORIAN	Los Colorados	Los Colorados		
	Ischigualasto			
	Los Rastros	Ischigualasto		
CARNIAN	Ischichuca	Los Rastros		
		Ischichuca		
LADINIAN			Ischigualasto	Ischigualasto
				?

Table 1. Recent chronological interpretations of some Triassic formations of Argentina.

ANALYSIS OF VERTEBRATE FAUNAS

Puesto Viejo Formation (Mendoza Province). — The fauna of these red sandstones comprises, so far as is now known, only therapsids of the infraorders Cynodontia and Dicynodontia. The cynodont *Pascualgnathus polanskii* Bonaparte (in press.b), known from very complete remains, is a diademodontid. It has affinities of great significance with *Trirachodon*, and of lesser significance with *Diademodon*. Among these points of similarity are important characters of the skull and jaws, the tooth row, the secondary palate, and so forth; in the axial region of the posteranial skeleton we also find good characters for the family assignation. *Pascualgnathus* is closer to African genera than to other cynodonts from South America or from other continents; it represents, therefore, an assemblage different from that common in South America, and provides new evidence of some type of vinculum between Africa and South America not detected in the case of other tetrapods from the South American Triassic.

Recent work on *Diademodon rhodesiensis* Brink (1963) and on a *Trirachodon*-like genus (Brink, 1963; Kitching, 1963) demonstrates that these genera survived beyond the end of the

Lower Triassic. They have been found in the Ntawere Formation, which immediately follows the *Cynognathus* Zone and is thus of probable Anisian age. As *Pascualgnathus* is but little advanced anatomically beyond *Trirachodon* and *Diademodon*, I have considered this genus to be also Anisian (Bonaparte, in press.b,c).

The dicynodont of this formation has been referred to the African genus *Kannemeyeria*, as *K. argentinensis* Bonaparte (in press.b), because of the great similarity between its skull and that of *Kannemeyeria* sp. (Watson, 1948, fig. 17) from the *Cynognathus* Zone. (*Kannemeyeria argentinensis* is a smaller species than the African representatives of the genus, so that posteranial similarities are less noticeable.) There are clear generic differences between *K. argentinensis* and other kannemeyerid genera. Until recent years, *Kannemeyeria* was unknown outside of the *Cynognathus* Zone, but a form referable to *Kannemeyeria* is cited by Kitching (1963) from the Ntawere Formation, and a *Kannemeyeria* from the Manda Formation of the Ruhuhu Valley in Tanganyika is reported by Cox (1965) and Brink (1963). It is thus apparent that *Kannemeyeria* survived into the Anisian; we can, consequently, consider *K. argentinensis* to be either Scythian or Anisian in age. The presence of *Pascualgnathus*, however, leads us to consider the therapsids of the Puesto Viejo Formation as Anisian.

Potrerillos Formation (Mendoza Province). — Fragmentary remains of a cynodont jaw constitute the only available tetrapod material from this formation. Minoprio (1954) studied these remains, and erected a new genus, *Colbertosaurus*, which he placed in the Ictidosauria. However, the principal anatomical feature used by Minoprio in his identification of *Colbertosaurus* as an ictidosaurian — the placement of the posterior part of the tooth row — is a common feature among the gomphodont cynodonts from the African Middle Triassic and the South American Middle or Upper Triassic; *Colbertosaurus* is thus more reasonably considered a gomphodont cynodont than an ictidosaurian (see Bonaparte, 1962). *Colbertosaurus* can best be compared with *Pascualgnathus*, from the Puesto Viejo Formation. The two have many features in common: the type of postcanine implantation, the number and size of the incisors, the large section of canines, the larger size of the postcanines in the middle of the tooth row, and the type of jaw constriction behind the canines. *Pascualgnathus* has eleven postcanines and *Colbertosaurus* nine.

It is evident that there is a significant, although limited, resemblance between the two genera. The Potrerillos Formation may therefore be considered, at least on the basis of present knowledge, as very close in age to the Anisian Puesto Viejo.

Cacheuta Formation (Mendoza Province). — From this formation we know two brachyopid labyrinthodonts, apparently representing two separate genera — *Pelorocephalus* Cabrera (1944) and *Chigutisaurus* Rusconi (1948). We also have the posteranial skeleton of a proterosuchian, *Cuyosuchus* Reig (1961), which was described by Rusconi in 1951 as a brachyopid.

Watson (1956) agreed that *Pelorocephalus* is a brachyopid, and accepted as valid the affinities claimed by Cabrera between *Pelorocephalus* and *Batrachosuchus* from the *Cynognathus* Zone. As Watson pointed out, brachyopid labyrinthodonts are known only from the Permian and Lower Triassic throughout the world.

These labyrinthodonts from the Cacheuta Formation require further study; it is possible that in the palatine features of the two genera there are similarities with *Batrachosuchus,* but the difference in skull height in *Chigutisaurus,* as well as its larger size, may indicate that the Argentinian brachyopids, perhaps because of peculiar ecological conditions, outlasted the Scythian. It would, of course, be out of the question to call them Keuper; tentatively we may consider them to be of Anisian age. *Cuyosuchus,* as mentioned above, is considered by Reig (1961) to be a proterosuchian; Hughes (1963) and Tatarinov (1961) agree with this designation. At present, all the more or less well known proterosuchians are of Scythian age, so that there is chronological agreement between them and the brachyopids. Thus, taking into consideration the possible special ecological conditions mentioned above, as well as some features of the *Chigutisaurus* skull, the fauna of the Cacheuta Formation is probably Anisian.

Sierra de las Higueras Formation (Mendoza Province). — The only fossil remains from this formation are a group of footprints representing five or six different forms, most of them observed and collected in 1963. Rusconi (1951b) studied a *Chirotherium* footprint showing an incomplete track of a hind limb and a probable track of the forelimb. Rusconi called them *C. higuerensis:* Peabody, in 1955, restudied these footprints, and assigned them to *C. barthi* from the Moenkopi Formation of the United

States. Reig (1961) and Casamiquela (1964) have demonstrated the weakness of such identifications, particularly as they are based on footprints which are far from clear. As mentioned above, Stipanicic (1957) considered the Sierra de las Higueras Formation to be Neoscythian-Eoanisian.

Among the footprints collected and observed in 1963 near Puesto de las Higueras, there is one similar to that of *Rigalites* Huene (1931) from the Los Rastros Formation. The others are referable to a lacertiform and to therapsids. It seems useful to examine the chronological position of *C. higuerensis* and the *Rigalites*-like genus together, rather than to examine *C. higuerensis* alone. A first point is that the structure of the foot of *Actosauroides* from the Ischigualasto Formation, which is known more or less in detail, is in agreement with the footprint of *C. higuerensis*. A second is that the footprints assigned to *Rigalites* from Las Higueras are probably not older than the *Rigalites* from the Los Rastros Formation. My interpretation is, of course, open to question, but it appears highly unlikely that the upper section of the Sierra de las Higueras Formation would be older than the Los Rastros. In consequence, I assume a Ladinian age for this formation.

Los Rastros Formation (San Juan Province). — The only known remains from this formation are good footprints of an archosaurian, *Rigalites ischigualastianus* Huene (1931). Huene considered them to be footprints of an ornithischian, but this is far from well established. Reig (1961), on the other hand, after study of the limbs assigned to *Saurosuchus* from the Ischigualasto Formation, believes that these footprints may well have been made by a pseudosuchian of great size, comparable to *Saurosuchus*. This idea appears to be more acceptable. Despite the fact that these footprints are very clear, their age is not easy to ascertain. Some inferences may be made from the fact that the Los Rastros Formation is overlain concordantly by the Ischigualasto Formation, the age of which is fairly well defined. On this basis, we conclude that the Los Rastros would not be younger than Upper Ladinian.

Ischigualasto Formation (San Juan and La Rioja provinces). — Cabrera (1944) first studied remains from the Ischigualasto Formation, which had been collected by Frenguelli. In recent years, a goodly number of papers on this fauna have been published, greatly increasing our knowledge of this, the richest Triassic tetrapod fauna of Argentina. These include papers by Reig (1959, 1961, 1963), Casamiquela (1960, 1962), Cox (1962,

1965), Romer (1962a), and Bonaparte (1962, 1963a-c, in press.a, b). The fauna of the Ischigualasto Formation is composed of six different groups; these will be discussed individually.

(1) Labyrinthodontia. *Promastodonsaurus bellmanni* Bonaparte (1963a) is represented by incomplete remains of the skull, jaws, and pectoral girdle. It has been assigned to the Capitosauridae, and closely resembles *Mastodonsaurus* from the Lower and Upper Triassic of Europe. As an indication of the chronology of the formation, it is, thus, of little value.

(2) Cynodontia. The cynodonts are very numerous in this formation, and are found in nearly all its levels. The carnivorous cynodonts are represented by a few specimens referred to *Chiniquodon* from the Santa María Formation of Brasil (Bonaparte, in press.a). The gomphodont cynodonts are *Exaeretodon* Cabrera (1944), *Proexaeretodon* Bonaparte (1963d), and *Ischignathus* Bonaparte (1963c); all three genera are found at approximately the same levels. *Exaeretodon* and the apparently somewhat less specialized *Proexaeretodon* are comparable with the Brasilian *Traversodon* and with *Scalenodontoides* from the Middle Triassic *sensu lato* of Africa (Crompton and Ellenberger, 1957). *Ischignathus* shows clear advances over the Brasilian and African Middle Triassic cynodonts, particularly in its palatine structure, which resembles that of the tritylodonts. Present knowledge indicates that the cynodonts from Ischigualasto are a little younger than those from Brasil; they are obviously older than the tritylodonts from the redbeds of Africa.

(3) Dicynodontia. The only known genus of this group is *Ischigualastia* (Cox, 1962, 1965). Cox believes that *Ischigualastia* gives us no decisive chronological data, as it could be considered either Ladinian or Carnian.

(4) Pseudosuchia. The genera of Pseudosuchia from this formation are *Saurosuchus* and *Proterochampsa* (Reig, 1959, 1961) and *Aetosauroides* and *Argentinosuchus* (Casamiquela, 1960, 1962). Reig considers that the rauisuchid ornithosuchian *Saurosuchus* is not only the largest genus of this family, but has a longer ischium and ilium, and a weaker femur than do *Prestosuchus* from Brasil or *Stagonosuchus* from Africa. We can assume that these characters represent anatomical advances over the Brasilian and African rauisuchids, comparable to the position noted in the cynodonts. *Proterochampsa* is considered by Reig as a true crocodilian. New materials of this genus, however, indicate the need for a reconsideration of its position, particularly because of the primitive palatine structure. *Aetosauroides*, well analyzed by Casamiquela (1962), shows important

similarities to *Aetosaurus* (from the German Keuper) in characters of the skull, vertebral column, pelvic and pectoral girdles, limbs, and armor. Some differences may be noted in the teeth, which indicate that *Aetosauroides* may be slightly more primitive than *Aetosaurus* (Casamiquela, pers. com.). *Aetosaurus* and the related genus *Stagonolepis* (*fide* Walker, 1961) are from the European Norian. In consequence, it is clear that *Aetosauroides*, if not actually Norian, cannot be too far from this age. *Argentinosuchus* is known only from a humerus, some fragments of the radius and ulna, and some dermal scutes, and is, tentatively assigned to the Stagonolepidae. As the principal diagnostic parts of this genus are missing, however, its chronology is dubious.

(5) Saurischia. Three genera of saurischian dinosaurs are known (Reig, 1963); a carnosaurian, *Herrerasaurus;* a coelurosaurian, *Triassolestes;* and *Ischisaurus*, of uncertain affinities. *Herrerasaurus*, known from good material of the posteranial skeleton, and from fragments of jaws which have been referred to it, is considered by Reig as more advanced, in some features at least, than other Triassic carnosaurians. *Triassolestes* is based on an incomplete skull and jaws, and some posteranial material. Reig reports some affinities with *Coelophysis* from the Upper Triassic, the only genus included in his comparison, and considers as possible the inclusion of *Triassolestes* in the Podokesauridae. The affinities of *Ischisaurus*, which is based on some posteranial remains and fragments of the skull and jaws, are uncertain; there are possible resemblances in the limb bones to Triassic pachypodosaurians.

Little can be inferred regarding chronological position from these incompletely known saurischians. Since all of the comparisons have been made with Upper Triassic forms, we have no valid arguments at present to consider them older than the Keuper; we may, then, assign them to the Carnian.

(6) Rhynchosauridae. Complete remains of these curious forms have been found at different levels of the Ischigualasto Formation. Until the present, unfortunately, no study has been made of them. Some general features of the skull and jaws of these rhynchosaurs resemble those of *Cephalonia* (or *Scaphonyx*) from Brasil. No chronological data can be drawn from these unstudied forms.

In several genera of the fauna of the Ischigualasto Formation, then, we find some advances over related Brasilian genera. It is also evident that the aetosaurid *Aetosauroides*, the traversodontid *Ischignathus*, and the three saurischians appear as forms

more related to Upper than to Middle Triassic faunas. On the other hand, the numerous cynodonts indicate a Middle Triassic age for this formation; their abundance, however, could be explained by supposing that ecological conditions permitted a later expansion of these forms. The advanced features of the cynodont *Ischignathus*, which has departed far from the known structure of the African Middle Triassic cynodonts, would support this view. The presence of both rhynchosaurs and cynodonts has been considered by Romer (1960, 1962b) as strong evidence that this is an upper Middle Triassic fauna — as noted above, "surely pre-Norian and not improbably pre-Carnian." But the fact that rhynchosaurs from the Norian or Carnian of India have been found associated with a phytosaur, with a form comparable to a coelurosaurian, and with prosauropod fragments (Jain, Robinson, and Chowdhury, 1964), makes his hypothesis of limited validity. In addition, rhynchosaurs have been reported from England, found in association with the supposedly Norian *Stagonolepis*. In consequence, we may consider the fauna of the Ischigualasto Formation as of Carnian age.

Los Colorados Formation (San Juan and La Rioja provinces). — In the past three years, much good tetrapod material has been found in this redbeds formation. This material is presently under study, but some general considerations are possible at this time. The Los Colorados Formation lies concordantly over the Ischigualasto Formation, and is about 800 m thick. At its base has been found a skull and jaws comparable to *Ischigualastia*, indicating the possibility of the survival of some genera common to the Ischigualasto Formation. But from the middle and upper sections of the Los Colorados we have found a completely different assemblage of tetrapods. At least three or four genera of prosauropods, some of great size, have been found. In addition, almost complete remains have been discovered of an aetosaurid closely related to *Aetosauroides*, but with more highly specialized teeth and cranial features; apparently this is a Norian fauna.

Our attempts to interpret the chronology of these Argentinian Triassic formations have been based on the currently accepted diagnoses of the Upper Beaufort and Stormberg Series of Africa, the Upper Scythian for the *Cynognathus* Zone, and so on. These attempts have been based solely on tetrapod remains from which excellent data have been obtained, particularly from the numerous forms comprising the fauna of the Ischigualasto Formation and from the two genera of the Puesto Viejo, which are

so closely comparable to African genera. This work raises the question of the age generally accepted for the Choiyoilitense and its correlations. Apparently this effusive series must be placed in the lower Middle Triassic, or else its correlations with Famatinense and Paganzo III are in need of re-examination.

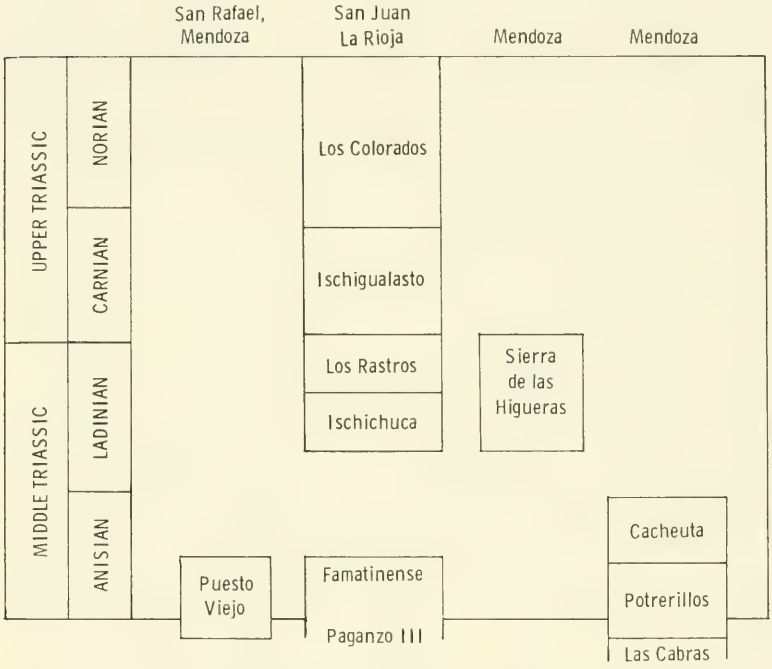

Table 2. A new attempt at chronology of some Triassic formations in Argentina.

LITERATURE CITED

BONAPARTE, J. F.

1962. Descripción del cráneo y mandíbula de *Exaeretodon frenguellii* Cabrera y su comparación. . . . Publ. Mus. Cienc. Nat., Mar del Plata, **1**: 135-202.

1963a. *Promastodonsaurus bellmanni* n.g. et n.sp., capitosáurido del Triásico Medio de Argentina. Ameghiniana, **3**: 67-78.

1963b. Descripción del esqueleto posteraneano de *Exaeretodon*. Acta Geol. Lilloana, **4**: 5-52.

1963c. Descripción de *Ischignathus sudamericanus* n.gen. et n.sp., nuevo cinodonte gonfodonte del Triásico Medio superior de San Juan, Argentina. Acta Geol. Lilloana, **4**: 111-128.

1963d. Un nuevo cinodonte gonfodonte del Triásico Medio superior de San Juan, *Proexaeretodon vincei*. Acta Geol. Lilloana, **4:** 129-133.

1963e. La familia Traversodontidae. Acta Geol. Lilloana, **4:** 163-194.

(In press.a) *Chiniquodon* Huene, en el Triásico de Ischigualasto, Argentina. Consideraciones sobre su asignación familiar. Acta Geol. Lilloana, **8:**

(In press.b) Sobre nuevos terápsidos Triásicos hallados en el centro de la Provincia de Mendoza, Argentina. Acta Geol. Lilloana, **8:**

(In press.c) Una nueva "fauna" Triásica de Argentina. Consideraciones filogenéticas y paleobiogeográficas. Ameghiniana.

Bonetti, M. I. R.

1963. Contribución al conocimiento de la flora fósil de Barreal, Dpto. de Calingasta (San Juan). Thesis, University of Buenos Aires.

Brink, A. S.

1963. Two cynodonts from the Ntawere Formation in the Luangwa Valley of Northern Rhodesia. Palaeont. Afr., **8:** 77-96.

Cabrera, A.

1943. El primer hallazgo de terápsidos en la Argentina. Notas Mus. La Plata (Paleont. No. 55), **8:** 317-331.

1944. Sobre un estegocéfalo de la Provincia de Mendoza. Notas Mus. La Plata (Paleont. No. 69), **9:** 69, 421-429.

Casamiquela, R. M.

1960. Noticia preliminar sobre dos nuevos estagonolepoideos argentinos. Ameghiniana, **2:** 3-9.

1962. Dos nuevos estagonolepoideos argentinos. Rev. Asoc. Geol. Argentina, **16** (3-4): 143-203.

1964. Estudios icnológicos. Gobierno Prov. Río Negro. Min. Asuntos Sociales. Buenos Aires, 229 pp.

Cox, C. B.

1962. Preliminary diagnosis of *Ischigualastia*, a new genus of dicynodont from Argentina. Breviora, Mus. Comp. Zool., No. **156:** 8-9.

1965. New Triassic dicynodonts from South America, their origins and relationships. Phil. Trans. Roy. Soc. London, B **248:** 457-516.

Crompton, A. W. and F. Ellenberger

1957. On a new cynodont from the Molteno beds and the origin of the tritylodonts. Ann. S. Afr. Mus., **44:** 1-14.

Groeber, P. F. C. and P. N. Stipanicic

1953. Triásico. *In:* Geografía de la República Argentina. Gaea, **2** (1): 7-141.

Huene, F. v.

1931. Die fossilen Fährten im Rhät von Ischigualasto in Nordwest-Argentinien. Paleobiol., **4:** 99-112.

1935-42. Die fossilen Reptilien des südamerikanischen Gondwanalandes. Munich, 332 pp.

Hughes, B.
1963. The earliest archosaurian reptiles. S. Afr. J. Sci., **59:** 221-241.

Jain, S. L., P. L. Robinson, and T. K. R. Chowdhury
1964. A new vertebrate fauna from the Triassic of the Deccan, India. Quart. J. Geol. Soc. London, **120:** 115-124.

Kitching, J. W.
1963. The fossil localities and mammal-like reptiles of the Upper Luangwa Valley, Northern Rhodesia. S. Afr. J. Sci., **59:** 259-264.

Minoprio, J. L.
1954. Theriodonte en el Triásico de Mendoza. An. Soc. Cien. Argentina, **157:** 31-37.

Peabody, F. L.
1955. Occurrence of *Chirotherium* in South America. Bull. Geol. Soc. Amer., **66:** 239-240.

Reig, O. A.
1959. Primeros datos descriptivos sobre nuevos reptiles arcosaurios del Triásico de Ischigualasto (San Juan, Argentina). Rev. Asoc. Geol. Argentina, **13:** 257-270.
1961. Acerca de la posición sistemática de la familia Rauisuchidae y del género *Saurosuchus* (Reptilia, Thecodontia). Publ. Mus. Cien. Nat. Mar del Plata, **1:** 73-114.
1963. La presencia de dinosaurios saurisquios en los "Estratos de Ischigualasto" (Mesotriásico superior) de las provincias de San Juan y La Rioja (República Argentina). Ameghiniana, **3:** 3-20.

Romer, A. S.
1960. Vertebrate-bearing continental Triassic strata in Mendoza Region, Argentina. Bull. Geol. Soc. Amer., **71:** 1279-1294.
1962a. La evolucion explosiva de los rhynchosaurios del Triasico. Rev. Mus. Arg. Cien. Nat., Cien. Zool., **8** (1): 1-14.
1962b. The fossiliferous Triassic deposits of Ischigualasto, Argentina. Breviora, Mus. Comp. Zool., No. **156:** 1-7.

Rusconi, C.
1948. Nuevos laberintodontes del Triásico de Mendoza. Rev. Mus. Hist. Nat. Mendoza, **2:** 225-229.
1951a. Laberintodontes Triásicos y Pérmicos de Mendoza. Rev. Mus. Hist. Nat. Mendoza, **5:** 33-158.
1951b. Rastros de patas de reptiles Pérmicos de Mendoza. Rev. Soc. Hist. Geogr. Cuyo, **3:** 1-14.

Stipanicic, P. N.
1957. El sistema Triásico en la Argentina. Internat. Geol. Congr., 20th, Mexico, Tr. Sec. 2: 73-111.

Tatarinov, L. P.
1961. Materiales de pseudosuchios de la URSS. Paleont. Zhurn. URSS, No. **1:** 117-132. [In Russian.]

WALKER, A. D.
1961. Triassic reptiles from the Elgin area: *Stagonolepis, Dasygnathus* and their allies. Phil. Trans. Roy. Soc. London, B **244:** 103-204.
WATSON, D. M. S.
1948. *Dicynodon* and its allies. Proc. Zool. Soc. London, **118:** 823-877.
1956. The brachyopid labyrinthodonts. Bull. Brit. Mus. (Nat. Hist.), Geol., **2:** 315-392.

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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA

II. SKETCH OF THE GEOLOGY OF THE RÍO CHAÑARES-RÍO GUALO REGION

BY ALFRED SHERWOOD ROMER AND JAMES A. JENSEN

TALAMPAYA BASIN

In the preceding article in this series an account was given of the joint La Plata-Harvard expedition of 1964-65 and the discovery during its course of an excellent fauna of Triassic reptiles in the region of the Chañares and Gualo rivers in La Rioja Province. The present paper is intended to give a rough outline of the geology of the collecting area so that the fossil horizon can be placed in its proper setting. Since our expedition was aimed solely at fossil collecting, proper instruments for geologic work were not part of our equipment, and mapping of the area was done by one of us (J.A.J.) with the aid of such instruments as could be improvised. Our map is thus provisional in nature; it is our hope that Argentinian geologists may make more definitive studies in this portion of an extremely interesting sedimentary basin.

Our area of concern is part of a basin of late Paleozoic and Mesozoic continental sediments located mainly in western La Rioja Province south of Villa Unión. No name has been applied to this region; we shall here term it the Talampaya Basin, because of the central position in it of the Campo de Talampaya.[1] Its boundaries, as regards presumed Triassic elements, at least, are outlined by Frenguelli in figure 1 of his 1948 discussion of the Argentinian "Rhaetic." To the east, the basin is bordered by the north-south range of the Sierra de Sañogasta, a southern

[1] Frenguelli (1948) speaks of the "Cuenca de Ischigualasto-Ischichuca," but this properly applies only to the southwestern portion of the basin.

continuation of the Nevada de Famatina, and by this sierra's southern terminations, such as the Sierra de Vilgo and the Sierra de Cerro Blanco; to the west, its boundary is the Río Bermejo, east of which the beds of the basin are sharply down-tilted, and to the north, its tributary, the Río Guandacol (or de la Troya). The sediments of the basin extend northward to the Villa Unión region. To the south, the basin narrows in the region of the little settlement of Los Baldecitos, where the southwestern-trending Sierra de Cerro Blanco approaches the Sierra de Valle Fertil, but (although the situation is obscured by a covering of Recent deposits) the sediments of the basin appear to be more or less in continuity with other late Paleozoic and Triassic beds extending eastward toward Paganzo and Patquia and possibly southward toward Valle Fertil in San Juan Province. Very probably, before the diastrophic movements which resulted in the rising of the Sierra de Sañogasta and the down-thrusting east of the Bermejo, the basin may have been of much greater extent, running from the Patquia district on the east to the Huaco region in San Juan Province to the west. The central portion of the basin is a nearly flat plain covered by Pleistocene sediments and Recent sands. The northern portion of this plain is drained by the Río Vinchina which at the south breaks through the hills at the west of the basin and joins the Río de la Troya (or Río Guandacol) to form the Río Bermejo. The barren Campo de Talampaya occupies most of the southern part of this plain. Its main drainage is the northward-flowing Río del Alto (or Arroyo Manero), with main tributaries from the east, in north-south sequence, including the Pagancillo, Medanos, Talampaya, Chañares, and Gualo rivers. Along the western margin of the basin extends a broken range of north-south hills which are essentially a sedimentary northward continuation of the Sierra de Valle Fertil, including the long Sierra Morada, Cerro Rajado, Cerro Bola, and Cerro Villa Unión; contained in the first of these is the depression of the Cuenca de Ischigualasto. On the east, the northern part of the plain is separated by well-developed foothills from the main Sierra de Sañogasta. East of the village of Pagancillo is the Loma de los Loros, composed of Tertiary deposits (de Alba, 1954, pp. 54-56), farther south the striking Sierra de los Tarjados, formed by Permo-Triassic sediments. South of the region of the Río Talampaya, the west flank of the Sierra de Sañogasta descends abruptly (due, presumably, to major faulting [Fidalgo, 1963]) to a sand-covered plain, averaging 10 to 15 kilometers in breadth, which slopes gently

westward toward the Campo de Talampaya. But for the last few kilometers before the campo is reached, erosion in the valleys of the Chañares and Gualo rivers, which drain this area, has in great measure removed the alluvial covering and developed a north-south series of foothills in which a considerable series of Permian and Triassic sediments is exposed.

It is this last mentioned area in which our fossil finds were made and with which the present paper is concerned. Figure 1 is a sketch of a portion of La Rioja and San Juan provinces to indicate the position of the small area covered by our geologic map.

We have in the first number of this series expressed our thanks to the numerous Argentinian geologists who aided our expedition by furnishing us with geological information and advice.

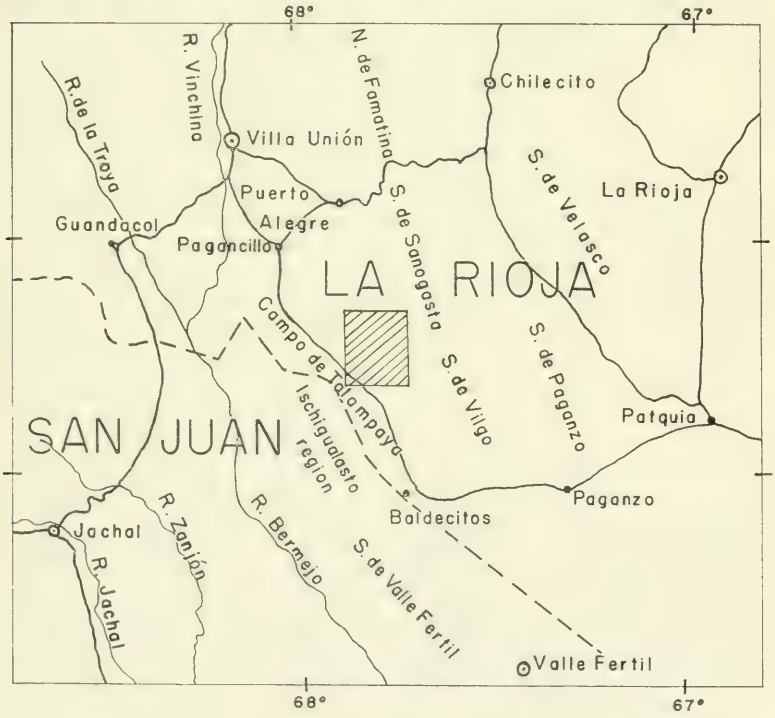

Fig. 1. Sketch map of parts of La Rioja and San Juan provinces, to show the position of the area studied. Rivers and principal roads indicated; provincial boundary in broken line. Scale approximately 1/1,200,000.

During the preparation of the present paper we have further corresponded, to our advantage, with Dr. Pedro N. Stipanicic of the Comisión Nacional de Energía Atomica, Dr. Hector F. de la Mota of the Yacimientos Petroliferos Fiscales, and Dr. Francisco Fidalgo of the Instituto Nacional de Geología y Minería.

In the entire area of the sedimentary basin described above, the population is small, due to great aridity (the average rainfall is about 2 inches [5 cm] per annum); railroads are entirely lacking, and roads few. Irrigation from the Río Vinchina has permitted the growth of population to about 3500 in the Villa Unión region; the water of the Río Pagancillo has allowed the development of a village of that name. But from Pagancillo southward some 90 kilometers to the little settlement of Los Baldecitos — an area of perhaps 5000 square kilometers — not a single inhabitant, not even a goat-herder, is to be found. At the north, Villa Unión is connected by national roads with Guandacol to the west, and, to the east, with Chilecito via Puerto Alegre and the Cuesta de Miranda; Pagancillo has road connections with both Villa Unión and Puerto Alegre. Until recently, almost no roads of any sort were present in the remainder of the basin; travel and exploration were exceedingly difficult, not merely because of the absence of highways, but also because of the nearly complete absence of fodder and water for the mules which formed the main means of transport.[1] A few years ago, however, a well-graded road, aimed to become eventually an international highway to Chile, was built from the railway junction of Patquia westward to Baldecitos, and thence north along the Campo de Talampaya to Pagancillo. From this highway (at kilometer post 100) a track has been worked out westward by Dr. Ramón de la Vega, via the Ischigualasto Valley, to the Los Rastros coal mine; at kilometer post 116 a track, traveled by occasional miners, runs eastward and northward along the plain at the foot of the Sierra de Sañogasta. In general, the sandy "river" channels, dry except after rare rainy-season showers, can be readily traveled by motors with four-wheel traction.

As said above, the presence here of a great basin of late Paleozoic and Mesozoic sediments was early recognized. Some early observations were made by Stelzner (1885), who traversed

[1] Note Bodenbender's emphatic (and italicized) warning (1911, p. 96): *"NOTA — A los futuros exploradores hago presente que no se puede contar — excepto anos de mucha lluvia — con sufficiente pasto para los animales,"* etc. There is, however, a mule track, of considerable antiquity and still used, from Jachal to Patquia, which crosses the Río Bermejo at Paso Ferreyro, traverses the Ischigualasto Valley, and continues on to the southeast.

the area in 1873, and later by Bodenbender, as noted in his publications of 1896, 1897, and 1902. The first published work of importance, however, was that of Bodenbender in 1911, in which he gave a general survey of the geology of southern La Rioja Province and adjacent regions of San Juan. It is to Bodenbender that we owe the invention of the term "Paganzo," commonly used by later writers in variable and often confusing fashion. Groeber in 1940 summarized what was then known of this region. De la Mota has done much valuable work, unfortunately unpublished, in various portions of the Talampaya Basin; Rigal, Harrington, and Ramaccioni have also worked here, but have not published; Fidalgo is currently studying the eastern portion as part of a survey of the geological Hoja Catizaco (which includes as well the Sierra de Sañogasta and territory to the east of it). The sediments of the most northerly part of the basin are described in de Alba's bulletin (1954) on the Villa Unión sheet of the geological map of Argentina. Heim published on coal deposits in this area in 1946 and 1947, and in his 1949 studies of the Los Rastros coal in the western part of the basin, contributed valuable observations on that area from his own observations, and to some degree from those of Ramaccioni. Most important are Frenguelli's studies of the area (1944a, b, c, 1945, and especially 1948), in which he appears to have relied greatly on the work of de la Mota and Ramaccioni. An excellent résumé of this work, as regards the Triassic beds, is given by Groeber and Stipanicic (1953). Recently Dr. Apolo Ortíz of the Y.P.F. has made important investigations, as yet unpublished, in the southwestern part of the basin. The greater part of previous studies has dealt with the western portions of the basin, west of the Campo de Talampaya; little study has been made of the eastern section, with which we are here concerned.

The general topographic features of the region of present interest are shown on the accompanying geological map. This is an area running for about 25 kilometers along the eastern border of the campo from the mouth of the Río Talampaya on the north to a point somewhat south of the Río Gualo. It extends eastward from the campo to the point, averaging about 10 kilometers, where the Permo-Trias beds become covered by the superficial deposits of a plain which slopes up eastward to the foot of the high mountains. At the northern end of the region studied, the Río Talampaya, which drains a considerable area of the sierra and its foothills, emerges south of the Sierra de los Tarjados onto the campo through a spectacular high-walled

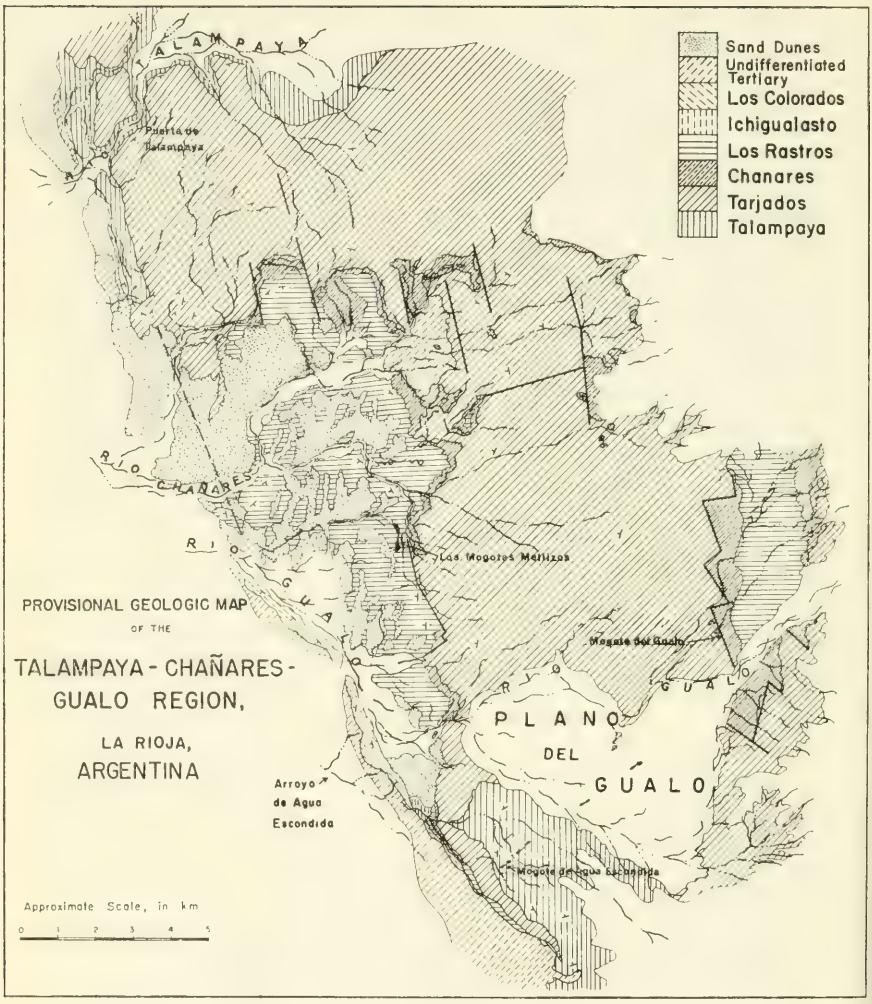

Fig. 2.

canyon, the Puerta de Talampaya. For some kilometers to the south of the river there is an elevated barren plain, with conspicuous exposures of red sandstones and with a series of parallel channels running northward to the Río Talampaya. South of this plain is the Río Chañares drainage, of which the lower part is notable for a considerable development of sand dunes which

obscure the underlying formations. A major southern branch of the river rises well to the east toward the sierra; in the region studied there are numerous small branches which gather into north and south forks, the two uniting a short distance east of the entrance of the river into the plain. The main branch of the Río Gualo arises at the western borders of the sierra, runs southwestward across the alluvial plain and, entering the region studied, flows along the northern margins of a flat, sandcovered plain, which we shall term the Plano del Gualo. Here it receives several short tributaries. One from the northeast has along its course the only perennial spring of any note in the region; a neighboring hill of red sandstone which serves as a landmark for the spring is the Mogote del Gualo. At the west border of the Plano del Gualo the river breaks through the sandstone cliffs which nearly surround this plain to enter a narrow north-south valley, bounded on the west by a ridge of red sandstone. This ridge is broken half-way along its length, and maps show the Gualo as turning westward through this gap. It may have done so at one time; currently, however, it follows the valley northward to the end of the sandstone ridge before debouching onto the plain only a short distance south of the Río Chañares.

Near the southwestern border of the Plano del Gualo is a prominent peak of volcanic rock, the Mogote de Agua Escondida. Arising in this region is a stream whose channel may be termed the Arroyo de Agua Escondida. This runs nearly directly westward out into the campo, and carves a deep channel along its course. It is of geological importance, since its walls show an almost complete section through all the formations present in the region studied.

The whole area is considerably faulted; only a few of the faults seen during our preliminary studies are shown on the map. In general, the beds in the north and east portions are relatively horizontal; to the west and south, dips in that direction become, on the average, increasingly steep until (in the region of the canyon of the Arroyo de Agua Escondida, as seen in Figure 2) the highest beds of the series are vertically placed and even somewhat overturned.

EL CHACHO FORMATION

Of the three successive stages into which Bodenbender divided his "Paganzo" series, the second, "Paganzo II," was applied to strata of presumably Permian age and, more especially, to a

series of red sandstones widespread in La Rioja Province — prominent, for example, from Patquia northward to Los Colorados station on the Chilecito railroad branch. Frenguelli (1946, p. 315, etc.) called these redbeds the Estratos de Patquia; I understand that Dr. Fidalgo plans to term them the El Chacho Formation — appropriately so, since the well-known cave, north of Patquia, where this war chieftain of the last century made his headquarters, is formed in this red sandstone series. There is no adequate fossil evidence to date these El Chacho beds, but there is no reason to doubt their Permian age. El Chacho redbeds are widespread in the Sierra de Sañogasta; some have been carried by diastrophism to high elevations in the range. West of the Sierra de Sañogasta, El Chacho redbeds are abundantly represented along the western slopes in the region of the Cuesta de Miranda and Puerto Alegre (de Alba, 1954), and are also present, in the northwestern portions of the basin, in Cerro Villa Unión and Cerro Guandacol. But on the east side of the basin, from the Río Talampaya southward, major faulting, as Fidalgo (1963) notes, appears to have been responsible for a steep western face of the Sañogasta range and absence of foothills of El-Chacho type. In consequence, these redbeds are not exposed in the area here studied, although they would presumably be encountered sub-surface.

TALAMPAYA FORMATION

Lowest of beds present in the area studied are those which we here term the Talampaya Formation — the name being given because of their extensive exposure in the valley of the Río Talampaya. The beds consist of rather uniform, pale reddish buff, sandy sediments, generally fine grained and finely bedded. Occasionally present, in seemingly random fashion, are cobbles, generally smoothly rounded, of crystalline material. In the Río Talampaya region they have a maximum size of about 80 millimeters; to the south, near the Agua Escondida, they are more numerous and larger, attaining a maximum of 30 centimeters in diameter.

The lower portion of the formation as exposed includes a cyclic repetition of soft and more resistant layers; in the upper 175 to 200 meters there are no resistant elements. Where the formation is broadly exposed at the surface, it weathers to give gently rounded to subangular profiles. Where, however, the upper beds are covered by the resistant basal conglomerate of

the overlying Tarjados Formation, the results are striking; the soft nature of the Talampaya beds results in the formation of sheer, vertical, fluted cliffs, the outlines of which follow precisely those of the overlying conglomerate. Such cliffs form much of the margin of the Sierra de los Tarjados north of the Río Talampaya; for several kilometers in the lower course of that river sheer cliffs of this sort, approximately 180-200 meters high, form the spectacular Puerta de Talampaya.

Presumably the Talampaya Formation succeeds the typical redbeds of "Paganzo II" in the Permo-Triassic sequence of the basin, but nowhere in the area visited by us is a normal contact between the two visible. The only contact seen during our exploration was that of about 1 kilometer along a normal fault, in alignment with the general fault system of the mapped area, but about 10 kilometers north of the upper boundary of the mapped area. Because of lack of knowledge of the base of the formation, its total thickness is unknown, but may be estimated to be at least 400 meters.

The Talampaya Formation is extensively exposed, as mentioned, in the valley of the Río Talampaya to the northeast of the mapped area and along the flanks of the Sierra de los Tarjados. West of the Puerta de Talampaya, a strip of exposure of the formation extends southward toward the Río Chañares for several kilometers along the base of cliffs formed by the Tarjados Formation. Apart from this, the Talampaya Formation is covered by younger beds over most of our region. To the south, however, southwest of the Plano del Gualo, it is present at the surface over a considerable area.

It is obvious that the Talampaya Formation is part of the complex of beds included by Bodenbender in his Paganzo system. It does not, however, correspond closely to any specific beds described by him in 1911. Possibly these strata may correspond to the fine, light brown, cross-bedded sandstones which Furque (1963) describes, in the Guandacol region, as part of the Ojo de Agua Formation, above the red sandstones which he considers equivalent to Bodenbender's "Paganzo II." Again, these beds may (cf. Turner, 1960) be equivalent to the lutites and marls which Bodenbender (1916) considers to be the basal portion of his "Estratos Famatinenses." Stipanicic (*in litteris*) suggests that the Talampaya, as well as the overlying Tarjados Formation, can be considered as part of "Paganzo III" or "Famatinense." It is possible that this set of beds may be comparable

to the "areniscas bandeadas" which de la Mota, in his unpublished thesis, includes as part of the third element (above a "Paganzo II" equivalent) in the series of beds described by him at Cerro Bola (the remainder of this set of beds include eruptives and porphyritic conglomerates).

TARJADOS FORMATION

Above the Talampaya Formation lie sandstones, of a coarse and resistant nature, which at the Arroyo de Agua Escondida have a thickness of about 385 meters. The name here given them is due to the fact that the lower part of these beds forms a broad covering over the Sierra de los Tarjados to the north of the area studied. South of the Río Talampaya, the Tarjados Formation is broadly exposed at the surface, covering perhaps half of the mapped area. In the southern part of the area there is generally a sharp division of the formation into lower and upper members, the lower mainly of red-colored sandstones, the upper predominantly white. However, the contrast between the two members is not so evident to the north. The lower, red member has a thickness of 130 meters in the measured section along the Arroyo de Agua Escondida. Throughout the area there is a basal conglomerate of variable thickness, but with a maximum of 2 to 3 meters, which lies unconformably above the Talampaya Formation. In the measured section there follow 10 meters of bright red, cross-bedded sandstone, then 35 meters of dull, reddish brown shale; this in turn is followed by 85 meters of bright red cross-bedded sandstones very similar to the basal section. Transitional here to the upper division, there are 4 meters of variegated sandstone, a thin limey nodular zone, and a further thin layer of sand and clay pebbles; above this are about 118 meters of sandstones, which are, for the most part, white in color. Cliffs of this upper division form much of the boundary of the Plano del Gualo; scraps of skull and postcranial materials, probably of a dicynodont, were found here in the transitional beds at two localities. A kilometer or so north of the boundary of the Plano del Gualo, a west-flowing northern tributary of the Río Gualo has excavated a deep canyon in the massive white sandstones of the upper division.

In the region of drainage into the Río Talampaya, at the north of the mapped area, the Tarjados beds are predominantly red in color. Here the lower sediments, above the basal conglomerate, are a dull red sandstone, 40 to 45 meters thick, with

alternate soft and resistant zones. They are overlain by 80 meters or so of bright ochre-red sandstones with almost no resistant strata. These erode in spectacular fashion to form fluted cliff faces, similar to the folds in a heavy drape. The appearance of these cliffs, apart from the difference in color, is similar to that of the cliffs of the underlying Talampaya Formation.

Whenever the entire thickness of the Tarjados surface is preserved, it is seen to terminate above in an uneven, undulating surface of hard, resistant materials containing a considerable quantity of chert, suggesting that this layer, typically about a half meter thick, results from some type of hydrothermal activity. This surface is frequently seen to be penetrated from above by small silica-filled tubules, averaging 2.5 centimeters in diameter, with a maximum of 5 centimeters, and penetrating to a depth as great as 3 meters. Their appearance suggests that we are dealing with root systems of plants which grew on the uneroded surface of the Tarjados before the beginning of the deposition of the overlying Chañares beds.

Bodenbender's "Paganzo III" was none too clearly defined by him, and, further, he appears to have been uncertain whether or not his "Famatinense" (Bodenbender, 1916) is an equivalent of "Paganzo III" (cf. Bodenbender, 1924; Turner, 1960). At all events, it seems probable that his intent was to apply the term "Paganzo III" primarily to beds of red sandstones lying above "Paganzo II" and below his "Rhaetic." It thus seems certain that the sandstones here named the Talampaya Formation are in the category of formations which he would term "Paganzo III." Stipanicic (*in litteris*) confirms our belief in this regard.

Below the "carboniferous" beds in the Ischigualasto region, which were termed Los Rastros and Ischichuca by Frenguelli and Heim, lie a series of red sandstones which are as yet imperfectly studied. Frenguelli (1948) considered them to be "Paganzo II," his Patquia Formation; Heim (1949) believes them to include both "Paganzo II" and "Paganzo III." I understand that Dr. Ortíz considers these beds to belong entirely to "Paganzo III," and that "Paganzo II" is lacking there. Quite surely, these beds are, in part at least, equivalent to our Tarjados Formation.

No comparable beds appear to have been present in Cerro Bola or the neighboring region of Cerro Guandacol, as studied by de la Mota (Frenguelli, 1946, 1948).

CHAÑARES FORMATION

Laid down on the undulate upper surface of the Tarjados beds are some 75 meters of light-colored beds, mainly fine volcanic tuffs, which form a striking contrast to all others in the area.

The basal beds of this formation, for a few meters overlying the Tarjados, are somewhat variable in nature, consisting of dull, pale green to dark buff or pinkish tuffs in which are included occasional thin pebble conglomerates with fossil vertebrate scraps and silicified plant materials, random beds of abundant limestone nodules with major diameters of up to 30 centimeters, and various compact nodular lenses composed of coarse sands, limestone, and chert, cemented into resistant masses of up to 8 meters in horizontal extent.

A short, if variable, distance above the base, the sediments become light-colored fine grained tuffs, with a somewhat bluish tinge, particularly in the lower part of the formation. They are well stratified; possibly aeolian, possibly, in part at least, lacustrine. With one exception, all of the numerous vertebrate fossils found in the Chañares were from the lowest 10 meters or so of the formation. A fraction of them were found directly embedded in the stratified tuffs; a large proportion, however, were found in grey-brown concretions which in many areas are abundant at this level; these consist of coarser tuffs, infiltrated by calcite and secondary silica.[1] These are flattened spherical structures, often with irregular outlines, and vary from 0.3 to 2.5 meters in diameter. In some areas they appear to be lacking in fossil content; in others (notably in the most northwesterly portion of the area of Chañares exposure) nearly every concretion contains reptilian material, sometimes with all or parts of two or three individuals in a single concretion. The remains are not always restricted to the limits of the concretion, and parts of a skeleton may extend into the surrounding stratified tuffs.

Above the fossil-bearing portion of the Chañares, the beds are nearly pure white in color, with a white concretionary zone well toward the top which tends to produce vertical cliffs.

At their top, the Chañares tuffs are followed without any unconformity by the beds here assigned to the Los Rastros Formation.

[1] We wish to thank Dr. Raymond Siever for studying samples of Chañares Formation sediments.

A main series of outcrops of the Chañares beds, somewhat interrupted by faults, follows the base of the Los Rastros Formation from the northwest part of the Río Chañares drainage, eastward and southward to the Río Gualo just beyond the point where it leaves the Plano del Gualo; faulting has caused the series to appear again to the eastward of this line, well up the courses of both the Río Chañares and Río Gualo.

Because of lack of unconformity, it would be possible to consider the Chañares beds a basal member of the Los Rastros. We believe, however, that they merit distinction as a separate formation, because of their distinctive lithology and because of their paleontological importance. I find in the available literature no description of Triassic beds which correspond at all closely to those of the Chañares. Presumably they may be equivalent to some portion of the sediments classed in other areas as part of the Ischichuca Formation (and which are presumably part of the Los Rastros Formation, as here defined). Our Chañares beds do not, however, compare with the basal part of the Ischichuca in the Río de la Peña region as described by Frenguelli (1948, p. 191 and fig. 29) on the basis of data furnished him by Ramaccioni, or as described by Heim (1949), nor do they compare closely with any part of the Ischichuca Formation in the type region of that formation, as described by Frenguelli (1948, pp. 200-208) mainly on the basis of de la Mota's unpublished work.

Future study of the fauna will presumably give evidence as to the age of the Chañares Formation. As seen in the field, the material suggested a somewhat later evolutionary stage than that seen in the *Cynognathus* Zone of South Africa. This zone seems certainly to be of early Triassic, Scythian, date (Watson, 1942, Lehman, et al., 1959). Hence the Chañares may be considered as either late Scythian or more probably Anisian in age.

LOS RASTROS FORMATION

The beds which we here include in the Los Rastros Formation occupy a considerable area in the lower parts of the Río Chañares and Río Gualo valleys east of the point at which these rivers debouch into the Campo de Talampaya. Over a large part of this area, however, these beds are covered by sand dunes, and they are variably tilted due to faulting. A further exposure of some extent is present, due to faulting, north of the main channel of the Río Gualo near the east edge of the mapped area.

The conformable contact between the Los Rastros and the underlying Chañares Formation is exposed over very considerable areas; on the other hand, a Los Rastros-Ischigualasto contact is visible only in the section seen in the Arroyo de Agua Escondida. Here the thickness of the formation is 216 meters (as contrasted with an estimated thickness of 600 meters for the combined Los Rastros-Ischichuca in the western part of the basin).

In general, the Los Rastros sediments consist of brown and tan sandstones interbedded with shales and clays, of various pale colors, and carbonaceous layers. Lack of continuous exposures due to sand dune coverage, and difficulty of correlation between various areas due to faulting and variable tilting, make it difficult to give a general description; it seems, however, certain that there is considerable variation in the beds from one region to another. Even over a short distance, such variations can be seen in the thickness of sandstone members. In some regions the sandstones are very prominent, in others — notably in the drainage of the south fork of the Río Chañares — shales and clays dominate; in this area, for example, shale and clay beds may reach a thickness of 30 meters or more without intercalation of any sandstone. There are a number of carbonaceous layers of variable thickness. Some of them apparently persist over a considerable portion of the mapped area; these contain abundant plant materials. In a zone in the upper portion of the formation there are several widespread beds of haematite which range in thickness from 2 to 10 centimeters. Occasional ironstone concretions in these layers contain fossil plant or fish remains of poor quality. In the upper Gualo area most of the beds in the formation appear to be thinner than they are farther to the west, suggesting (together with a relatively high ratio of sandstones to clays) a region of marginal deposition. On the south side of the Río Chañares canyon, near its mouth, there is a notable display of a cyclical type of deposition which appears to be to some degree characteristic of the formation as a whole. Here four cycles can be seen, each consisting, in order from top to bottom, of sandstones, sandy shales, carbonaceous shales, and clays, followed below by the sandstone of the next cycle. These cycles have thicknesses of 10 to 25 meters.

In the northwestern part of the Talampaya Basin, de la Mota has distinguished an Ischichuca Formation; Heim (1949), in his description of the Río de la Pena region, somewhat arbitrarily divides the carbonaceous beds lying between the Ischigualasto Formation above and the redbeds below into the Ischichuca and

Los Rastros formations. This is also done by Frenguelli (1948) who, it seems, was personally familiar only with the upper portion of the Los Rastros Formation in the Cerro Bola region. I am informed that current belief is that the whole series of carbon-bearing beds in the La Peña region should be considered a single unit, the Los Rastros Formation. We likewise see no reason why the similar (and much thinner) beds in our area of interest should not be considered a unit, although, as mentioned earlier, the underlying Chañares Formation may be in some fashion equivalent to part of the Ischichuca.

ISCHIGUALASTO FORMATION

In the western portion of the Talampaya basin, the Ischigualasto Formation is extensively exposed; it was described in some detail by Frenguelli in 1948, and has become well known through the discovery in it of an abundant vertebrate fauna. On the east side of the basin, however, it is seen only in the walls of the Arroyo de Agua Escondida; here the Ischigualasto is present in proper sequence between the Los Rastros and Los Colorados Formations, the beds tilted at an angle close to the vertical. Presumably they continue to the north, in the valley in which the Río Gualo flows northward for some distance east of the ridge formed by the Los Colorados. It can be assumed that this valley formed because the lack of resistant layers in the Ischigualasto beds resulted in greater erosion of them than of the sandstones of the Los Colorados; there is no Ischigualasto exposure here, due to a covering by Recent materials. In contrast to the much greater thickness, of perhaps 400-500 meters, in the Ischigualasto Valley, the beds as measured in the Arroyo are only 175 meters thick. We found no fossils in the limited available exposures. The sediments, however, compare closely with those in the type area, except that there is an almost complete absence here of the resistant sandstone layers encountered at intervals in the type area. As at Ischigualasto, the beds contain pale purple, grey, and tan joint-clays interbedded with pale maroon, green, and yellow siltstones. Two or three thin beds of nodular limestone are present, one of which includes some poorly preserved plant material.

Below, there is a sharp contrast between the Ischigualasto sediments and the interbedded hard sandstones and shales of the Los Rastros Formation. Above (as in the Ischigualasto Valley)

there is, over a short vertical distance, a transitional zone between the Ischigualasto Formation and the overlying Los Colorados of interbedded sands and silts grading in color from greys and yellow-tans into dull reddish brown. It was apparently such transitional beds, between Cerro Morado and the southern end of the Los Colorados in the Ischigualasto Valley, which led Bodenbender (1911) to insert a "Jurassic" phase into his sequence in that region ("perfiles III y IV" and p. 97).

As noted in the previous paper in this series, the fauna of the Ischigualasto Formation is essentially Middle Triassic; it is, however, difficult to determine whether it should be considered as parallel to the Ladinian or to the Carnian of the marine Triassic sequence.

LOS COLORADOS FORMATION

The massive red sandstones which bound the Ischigualasto Valley to the east and form a nearly continuous range of hills along the western side of the Campo de Talampaya were termed the Estratos de Gualo by Frenguelli (1948, pp. 170-174), on the assumption that the red sandstones forming the Mogote del Gualo were of similar age. However, this is not the case, as was pointed out by de la Mota to Groeber and Stipanicic; at his suggestion, they renamed these sandstones the Los Colorados Formation (1953, p. 88). In contrast to the prominence of the Los Colorados on the western side of the Campo de Talampaya, their exposure on the eastern side is limited to a low ridge extending only from the Arroyo de Agua Escondida north to the point where the Río Gualo debouches onto the plain. As seen at the Arroyo de Agua Escondida, the Los Colorados sandstones are almost vertical. Only 95 meters of sediments are present; they are immediately followed by Tertiary deposits having an angular discordance of about 20°. Since the thickness here is much less than in the Ischigualasto region across the campo, it seems certain that much of the thickness of the formation was eroded at some time before the deposition of the Tertiary, and that it is only the basal portion of this sandstone series that is preserved. The beds consist of soft, dull red sandstones interbedded with silts and clays of the same color. One thin but resistant layer of lime nodules forms the highest portion of the ridge.

Bodenbender (1911), for no strong reason, considered these redbeds to be Cretaceous in age — "Cretácea superior andina."

Their earlier age was recognized by later authors; Frenguelli assigned them, together with still lower formations, to the Rhaetic (1948, p. 302), and Groeber and Stipanicic likewise considered them as Rhaetic in 1953. No fossils have been described from these beds; however, Sr. Bonaparte of the Instituo Lillo of Tucumán has recently discovered dinosaur remains of Upper Triassic type in the Los Colorados beds on the west side of the Campo de Talampaya. It thus seems reasonable to compare them in general with other redbeds, generally considered Norian, which conclude the Triassic series in various other parts of the world, such as the redbeds of South Africa, the Lufent series of China, the Upper Keuper of Europe, and part, at least, of the North American Triassic redbeds.

TERTIARY

Bodenbender (1911, perfil III, etc.) assumed, apparently because the red Los Colorados sediments appear on both margins of the Campo de Talampaya, that these rocks directly underlay the Campo. This is not the case. At the mouth of the canyon of the Arroyo de Agua Escondida there is seen a thick series of Tertiary sediments to the west of the Los Colorados which are not merely turned, like them, into a vertical position, but are even overturned beyond the vertical to about 20° as a result of major late Tertiary or Pleistocene diastrophism. If there is any continuity between the Los Colorados on the two sides of the campo, this must be at a considerable depth. We have not studied these Tertiary sediments, which, like those of the Loma de los Loros farther north, are presumably of the sort customarily termed "Estratos Calchaqueños."

ERUPTIVE ROCKS

In the northwestern part of the Permo-Triassic basin, volcanic rocks are prominent. De la Mota, for example, in his unpublished works on Cerro Bola describes thick intrusions of melaphyrite; Frenguelli (1944a) likewise describes similar intrusions in the sediments of Cerro Guandacol; and farther to the south on the western basin margin, Cerro Rajado owes its name to its partial bisection by a conspicuous but eroded dyke; still further eruptives are present in the Cerro Morado area. In the area here studied, in contrast, there are few evidences of such activity, but there are present three dykes:

(1) In the southwestern portion of the mapped area there appears a dyke, running in an ENE direction, which forms a notable elevation, the Mogote de Agua Escondida; a lesser elevation lies just to the east of this and, following a gap, two further exposed sections lie in the Plano del Gualo. The dyke is composed of green crystalline material which is less resistant to erosion than the metamorphosed sediments immediately adjacent. The Agua Escondida is not a true spring, but a catch-basin for water in the hollow formed in the dyke by erosion in the low spot between the mogote and the lesser elevation to the east of it. Part way up the side of the mogote there adheres a mass of modified sedimentary rock including a portion of the contact between the Talampaya and Tarjados formations, thus giving a maximum date for dyke formation. However, the mogote is capped by a basalt-like rock, dense, brown in color, and giving a conchoidal fracture, indicative of its extrusive nature and suggesting the formation of the dyke posterior to erosion of higher, Triassic sediments in the basin, presumably in Tertiary times.

(2) In the northeastern portion of the Gualo Basin shown in our map are modest exposures of a SW-NE trending dyke penetrating Los Rastros sediments.

(3) Along a high divide between the Gualo and Chañares drainages, a few kilometers east of the Campo de Talampaya, are two conspicuous peaks, close together, and rising abruptly about 100 meters above the Los Rastros beds at their bases, which may be termed Los Mogotes Mellizos. These have superficially the appearance of volcanic plugs, but seem to be in reality portions of a dyke. The upper portion of the intrusive material, apparently basaltic in nature, contains considerable fragments of sedimentary rocks apparently originating in surrounding beds. The baking of the sediments about the base of the dyke is not extensive; the situation as a whole suggests that little if any extrusive surface action occurred.

LITERATURE CITED

ALBA, E. DE

1954. Descripción geológica de la Hoja 16c, Villa Unión (Provincia de La Rioja). Bol. Dir. Nac. Min. (Argentina), **62:** 1-81.

BODENBENDER, G.

1896. Beobachtungen über Devon- und Gondwana-Schichten in der argentinischen Republik. Zeitschr. Deutsch. Geol. Ges., **48:** 743-807.

1897. Devono y Gondwana en la República Argentina. Bol. Acad. Nac. Cienc. Córdoba, **15:** 201-252.

1902. Contribución al conocimiento de la Precordillera de San Juan, de Mendoza, y de las Sierras centrales de la República Argentina. Bol. Acad. Nac. Cienc. Córdoba, **17:** 203-261.

1911. Constitución geológica de la parte meridional de la Rioja y regiones limítrofes (República Argentina). Bol. Acad. Nac. Cienc. Córdoba, **19:** 1-220.

1916. El Nevado de Famatina. Bol. Acad. Nac. Cienc. Córdoba, **21:** 100-182.

1924. El Calchaqueño y los estratos de la Puna de Penck. Bol. Acad. Nac. Cienc. Córdoba, **27:** 405-468.

FIDALGO, F.

1963. Algunos rasgos tectónicos y geomorfológicos de la Sierra de Sañogasta-Vilgo (Prov. de la Rioja). Rev. Asoc. Geol. Argentina, **18:** 139-153.

FRENGUELLI, J.

1944a. Apuntes acerca del Paleozoico Superior del noroeste argentino. Rev. Mus. La Plata, (NS) Sec. Geol., **2:** 213-265.

1944b. La serie del llamado Rético en el oeste argentino. Notas Mus. La Plata, Geol., **9:** 261-269.

1944c. Excursiones al territorio del Neuquén y a las provincias de Mendoza y La Rioja. Rev. Mus. La Plata, (NS) Sec. Oficial, 1943 (1944): 87-102.

1945. Viaje a la Precordillera. Rev. Mus. La Plata, (NS) Sec. Oficial, 1944 (1945): 157-169.

1946. Consideraciones acerca de la "serie de Paganzo" en las provincias de San Juan y La Rioja. Rev. Mus. La Plata, (NS) Sec. Geol., **2:** 313-376.

1948. Estratigrafía y edad del llamado Rético en la Argentina. Gaea, An. Soc. Argentina Est. Geogr., **8:** 159-309.

FURQUE, G.

1963. Descripción geológica de la Hoja 17b-Guandacol. Bol. Dir. Nac. Geol. Min. (Argentina), **92:** 1-104.

GROEBER, P. F. C.

1940. Descripción geológica de la Provincia de la Rioja. *In:* Aguas Minerales de la República Argentina, **6:** 17-29.

GROEBER, P. F. C. AND P. N. STIPANICIC

1953. Geografía de la República Argentina, II (Primera Parte): Triásico. Buenos Aires. Pp. 13-141.

HEIM, A.

1946. El carbon de la mina "La Negra," Villa Unión (La Rioja) y su posición tectónica. Bol. Dir. Min. Geol. (Argentina), **60:** 1-19.

1947. El carbon del Río Huaco (Provincia de San Juan) y su posición tectónica. Bol. Dir. Min. Geol. (Argentina), **62:** 1-18.

1949. Estudio geológico del carbon "Rético" y del Valle de la Peña (provincias de San Juan y La Rioja). Bol. Dir. Gen. Ind. Min., **69:** 1-31.

LEHMAN, J.-P., C. CHATEAU, M. LAURAIN, M. NAUCHE

1959. Paléontologie de Madagascar. XXVIII. Les poissons de la Sakamena moyenne. Ann. Paléont., **45:** 177-219.

STELZNER, A. W.

1885. Beiträge zur Geologie und Palaeontologie der argentinischen Republik. I. Geologischer Theil. Cassel & Berlin, 329 pp.

TURNER, J. C. M.

1960. Estratigrafía del tramo medio de la Sierra de Famatina y adyaciencias (La Rioja). Bol. Acad. Nac. Cienc. Argentina (Córdoba), **42:** 77-126.

WATSON, D. M. S.

1942. On Permian and Triassic tetrapods. Geol. Mag., **79:** 81-116.

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BREVIORA

Museum of Comparative Zoology

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A NEW HISPANIOLAN GECKO

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Recent collecting in Haiti yielded a single specimen of an undescribed species of *Sphaerodactylus* from the western part of the Massif de la Hotte on the Tiburon Peninsula. I wish to express my appreciation to Dr. Albert Schwartz, who sponsored my collecting in Haiti (February to April of 1966), which resulted in the discovery of this new species. The abbreviation MCZ denotes the Museum of Comparative Zoology, and ASFS denotes the Albert Schwartz Field Series.

In reference to its most salient distinguishing character, this new gecko may be known as

SPHAERODACTYLUS ELASMORHYNCHUS[1] new species

Holotype: MCZ 81119, a female, taken ca. 5 km (airline) SSE Marché Léon, Dépt. du Sud, Haiti, at an elevation of 2600 feet (790 meters), on 15 March 1966 by Richard Thomas. Original number ASFS V9353.

Diagnosis: A species of *Sphaerodactylus* distinguished by: 1) much enlarged supranasals and postnasals[2] which abut against the rostral and labials to form a continuous, platelike covering over most of the snout; 2) a finely granular dorsal scalation; 3) large, smooth, imbricate ventral scales; and 4) a dorsal coloration of small orange ocelli on a dark brown ground color. The first character distinguished *elasmorhynchus* from all other known species of *Sphaerodactylus.*

Description of holotype (Fig. 1): Snout-vent length 17 mm; tail (unregenerated) 17 mm. Rostral with a median crease; postnasals enlarged, roughly trapezoidal with bases towards anterior

[1] From the Greek, *elasmos*, plate, and *rhynchos*, snout.

[2] Although I could not see a definite nasal scale, even under high magnification, I have called the large scale behind the naris the postnasal because of its position (see Smith, 1946, fig. 27).

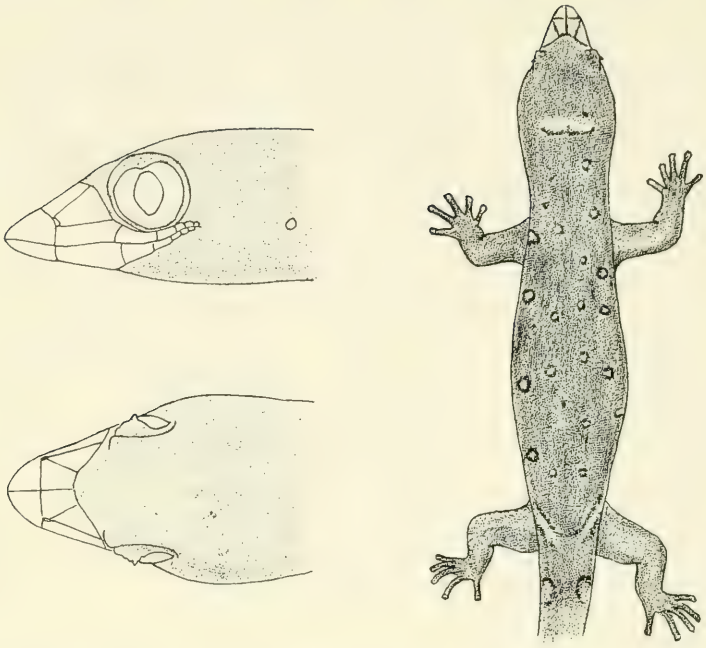

Fig. 1. Holotype of *Sphaerodactylus elasmorhynchus*: lateral and dorsal views of head and full dorsal view.

edges of orbits and ventral long sides sutured with upper edges of first supralabials; two large, platelike, roughly trapezoidal supranasals with their bases abutting against posterior edge of rostral and their lateral edges against dorsal edges of postnasals. Upper labials to mid-eye, two. Rostral, supranasals, postnasals and labials form platelike covering to snout. Scales of snout behind platelike covering swollen, subimbricate to imbricate, and keeled. Scales of top of head and on body granular, subimbricate, keeled, more swollen and more erect on flanks than middorsally; dorsal scales, axilla to groin, 56 (an injury on the venter prevents the taking of midbody and longitudinal ventral counts); 1-2 large hair-bearing (3 hairs, at most) scale organs on the tip of each scale. Scales on anterodorsal parts of limbs flattened and imbricate. Gular scales granular; ventral scales large, rounded, flattened, smooth and imbricate; transition between the two on posterior part of neck abrupt. Dorsal scales of tail flattened, flat-lying, acute, keeled and imbricate; ventral scales of

tail flattened, flat-lying, rounded and smooth, midventral row enlarged. Fourth toe lamellae 10.

Coloration: In life the type was dark brown with dark-edged, orange-centered ocelli on body and tail. The ocelli are arranged in six irregular longitudinal rows on the body; those of the dorsolateral rows are largest and most prominent; those of the paramedian and ventrolateral rows are smaller and less distinct. The occiput bears a pair of transversely elongate light markings, and a faint pair of forked, dark, postocular stripes was noted in life. The sacrum has a pair of enlarged, diagonal light markings whose dark medial margins unite to form a U-shaped sacral figure. Two dorsal rows of ocelli occur on the tail. The throat is lightly pigmented and has faint lighter longitudinal streaks; the venter is very heavily pigmented but has light central areas to many of the scales.

Comparisons: The enlarged platelike scales of the snout distinguish this species from all other known *Sphaerodactylus*. Also distinctive are the size difference between the dorsal and ventral scales and the relatively abrupt transition from gular granules to ventral scales. Head length (ear to tip of snout) has been plotted against snout-vent length for five species of *Sphaerodactylus* in addition to the type of *elasmorhynchus* (Fig. 2). The value plotted for the type of *elasmorhynchus* falls with the values for adult specimens of small species (*S. n. nicholsi* Grant and *S. parthenopion* Thomas), rather than with the values plotted for juvenile specimens of larger species (*S. cinereus* Wagler, *S. roosevelti* Grant, *S. difficilis* Barbour). Thus it appears that the type of *elasmorhynchus* is an adult or subadult, not a juvenile, and represents a small-sized species.

The distinctness of *S. elasmorhynchus* prevents an assessment of its relationships at this time; it is not obviously a member of any of the recognized groups of the genus. Although *elasmorhynchus* has granular dorsal scales, it differs strongly from all members of the predominantly granular scaled *decoratus* group in the characters mentioned above, and apparently in size also (for a review of the *decoratus* group, see Thomas and Schwartz, 1966). Of the known species of Hispaniolan sphaerodactyls, *S. cinereus* is the only other one having granular dorsal scales, but it too has no evident affinities with *elasmorhynchus*. The large hair-bearing scale organs of *elasmorhynchus* are characteristic of other granular scaled *Sphaerodactylus;* the small number per scale is probably a reflection of the small size of the species.

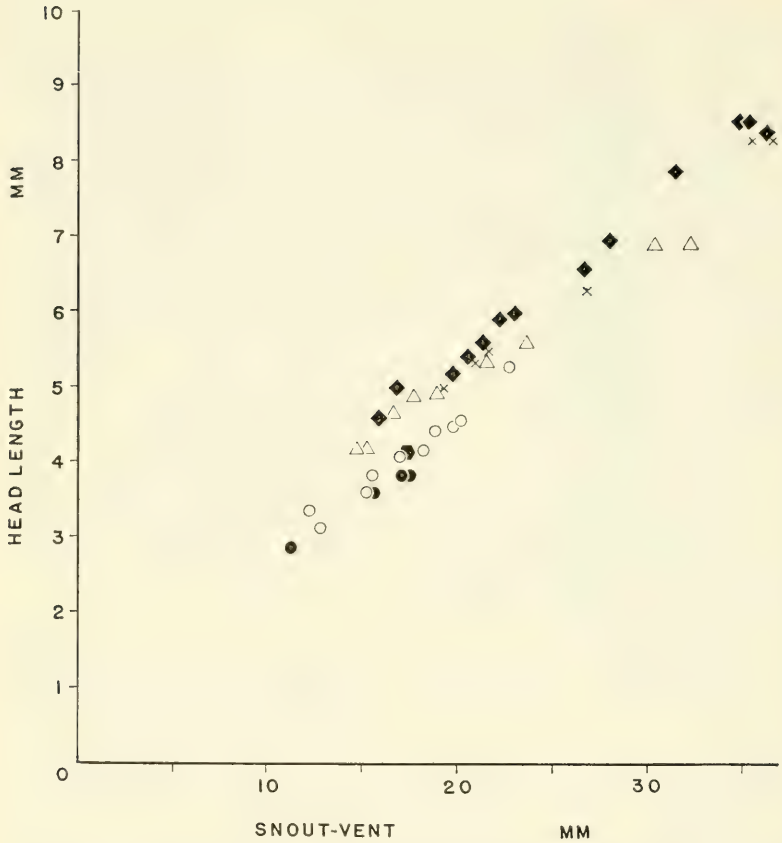

Fig. 2. Scatter diagram of head length (anterior border of ear to tip of snout) versus snout-vent length for six species of *Sphaerodactylus*: solid rhombs, *S. cinereus;* hollow triangles, *S. difficilis;* crosses, *S. roosevelti;* hollow circles, *S. n. nicholsi;* solid circles, *S. parthenopion;* solid hexagon, type of *S. elasmorhynchus.* For each species, aside from *elasmorhynchus*, the range of values plotted includes near-hatchling juveniles through mature adults.

Grant (1957) has shown that the enigmatic *S. nigropunctatus* Gray, known from a single type of unknown provenance, is a granular scaled form. However, references to the snout scalation of *nigropunctatus* in Grant (1957), and a drawing of its snout (Boulenger, 1885, pl. 18), indicate that it has the normal *Sphaerodactylus* snout scale configuration; the type is also large in size.

Remarks: The type of *S. elasmorhynchus* was found among the roots of a standing but rotten tree on the side of a ravine filled with a jumble of limestone rocks and boulders. Although the surrounding countryside was much cut over, the ravine was overgrown with mesic vegetation. Also taken at this locality were specimens of the relatively little known *Anolis monticola* Shreve. No other sphaerodactyls were found at this locality. Of the named Hispaniolan species, *S. copei* Steindachner and *S. cinereus* are the only ones occurring in this general region of Haiti.

LITERATURE CITED

Boulenger, George Albert

1885. Catalogue of the lizards in the British Museum (Natural History). London. 2d ed., vol. 1, pp. i-xii, 1-436.

Grant, Chapman

1957. The status of *Sphaerodactylus nigropunctatus*, a neotropical gecko. Nat. Hist. Misc., Chicago Acad. Sci., No. **158**, pp. 1-4.

Smith, Hobart M.

1946. Handbook of lizards. Comstock Pub. Co., Ithaca, New York, pp. i xxi, 1-557.

Thomas, Richard, and Albert Schwartz

1966. The *Sphaerodactylus decoratus* complex in the West Indies. Brigham Young Univ. Sci. Bull., Biol. Ser. (In press.)

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BREVIORA

Museum of Comparative Zoology

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PRELIMINARY DESCRIPTIONS OF NEW HONEY-EATERS (AVES, MELIPHAGIDAE)

BY FINN SALOMONSEN[1]

For many years I have been engaged in a study of the Meliphagidae, mainly based on the outstanding collections in The American Museum of Natural History, New York (AMNH). During this study it appeared that a number of forms were undescribed; these forms are named and described in the present paper. The descriptions must be regarded as preliminary, and more detailed documentation will appear in a monograph of the Honey-Eaters, now in preparation. The descriptions had to be published now, however, in order to incorporate the new forms in my review of the Meliphagidae in Peters' Checklist of Birds of the World, Volume 12, which is now in press.

MELILESTES MEGARHYNCHUS BRUNNEUS new subspecies

Type: AMNH No. 294369, adult male; Siwi, Arfak Mountains, New Guinea; May 2, 1928; Ernst Mayr collector.

Diagnosis: Darker and more brownish than nominate *megarhynchus* (type locality: Aru Islands). The upper parts are warm brown without the olive tinge of *megarhynchus*, the under parts are darker brownish grey than *megarhynchus*, not so olive, and the abdomen and under tail-coverts are darker and warmer cinnamon brown. Also, the upper parts of the head are darker brown with broader blackish striation.

Range: Misol and Salawati in the western Papuan Islands, Vogelkop and Onin Peninsula in northwestern New Guinea, in the Weyland Mountains tending towards nominate *megarhynchus*.

[1] Zoological Museum, Copenhagen.

Oedistoma pygmaeum waigeuense new subspecies

Type: AMNH No. 301021, adult male; Waigeu Island; June 5, 1931; G. Stein collector.

Diagnosis: Differs from nominate *pygmaeum* (type locality: Arfak Mountains, New Guinea) in having crown and nape dark grey, strongly contrasting with green upper parts (in nominate *pygmaeum* crown green, only slightly darker than upper parts), throat and breast paler grey than in nominate *pygmaeum*. Proportions smaller. Wing length of adult males 45-46 mm, in *pygmaeum* 47-51 mm; bill 11.8-12.8 mm, in *pygmaeum* 13-14 mm.

Range: Waigeu Island, in the western Papuan Islands.

Oedistoma pygmaeum flavipectus new subspecies

Type: AMNH No. 422241, adult male; Wuroi, Oriomo River, British Papua (western division), southern New Guinea; Feb. 10, 1934; R. Archbold and A. L. Rand collectors.

Diagnosis: Upper parts distinctly paler green than in nominate *pygmaeum*, crown and nape of the same green color as rest of upper parts, under parts strongly suffused with yellow, abdomen and flanks with more yellow than in nominate *pygmaeum* and *waigeuense*. Proportions as in the nominate form.

Range: Southern New Guinea, from Etna Bay to Milne Bay.

Oedistoma pygmaeum olivascens new subspecies

Type: Mus. Comp. Zool., Cambridge, Mass., No. 167910, adult male; Upper Watut River, southeastern New Guinea; July 27, 1932; H. Stevens collector.

Diagnosis: Very similar to nominate *pygmaeum*, but under parts with a conspicuous greyish olivaceous tinge and upper parts slightly darker.

Range: Northern coast of southeastern New Guinea, from Milne Bay to Huon Peninsula.

Lichmera incana mareensis new subspecies

Type: AMNH No. 337641, adult male; Maré Island, Loyalty Islands; Nov. 8, 1937; L. Macmillan collector.

Diagnosis: Very similar to *L. i. poliotis* (type locality: Loyalty Islands, restricted here to Lifu Island), but under parts darker grey, and lower breast and abdomen with much more yellow. Not differing from *poliotis* in measurements.

Range: Maré Island, Loyalty Islands.

LICHMERA INCANA GRISEOVIRIDIS new subspecies

Type: AMNH No. 212924, adult male; Lopevi Island, New Hebrides; Aug. 9, 1926; J. G. Correia (The Whitney South Sea Expedition) collector.

Diagnosis: Very similar to *L. i. flavotincta* (type locality: Erromanga, New Hebrides), but paler throughout; crown paler grey, upper parts paler and less brownish green, and, particularly, under parts paler with less yellowish olive on lower breast and abdomen. Differs from *marcensis* in its much larger proportions, but plumage coloration very similar, although the under parts are slightly darker grey with the yellow tinge less pronounced.

Range: Central New Hebrides (Efate, Makura, Mai, Tongoa, Epi, Lopevi, Pauuma, Ambrym, and Malekula).

MYZOMELA NIGRITA NIGERRIMA new subspecies

Type: AMNH No. 422677, adult male; Long Island, off the northeastern coast of New Guinea; Dec. 2, 1933; W. F. Coultas (The Whitney South Sea Expedition) collector.

Diagnosis: Similar to *M. n. ernstmayri* (type locality: Manu (= Allison) Island, west of Ninigo Islands), but darker throughout. Under wing-coverts black like the axillaries, inner linings of remiges darker greyish and almost indistinguishable from the greyish black ground color of the remiges, plumage of adult males more shining black and with darker greyish black feather bases. Proportions distinctly larger than in *ernstmayri*. Wing length of adult males 77-79 mm, in *ernstmayri* 75-77; adult females 71 mm, in *ernstmayri* 66-69 mm.

Range: Long Island, off the northeastern coast of New Guinea.

MYZOMELA CARDINALIS ASUNCIONIS new subspecies

Type: AMNH No. 692934, adult female; Asuncion Island, in the northern Marianas Islands; June 1904; Owston's Japanese collectors.

Diagnosis: Adult males do not differ from *M. c. saffordi* (type locality: Guam Island, southern Marianas Islands) except by larger proportions. Wing length of adult males 76-79 mm, in *saffordi* 70-75 mm. Adult females differ strikingly from *saffordi* by having the red color strongly reduced, and by having light, greyish yellow under parts. Upper parts dark olive brown, with

the feathers of back and rump (but not mantle and neck) broadly edged with red, feathers of forehead and nape edged with dull red, chin dull red, under parts greyish yellow with a reddish wash on throat and chest. The only adult female ever collected (the type specimen) in its color pattern somewhat resembles immature birds of *saffordi*, but in all respects appears to be an adult bird.

Range: Northern Marianas Islands (Asuncion, Agrihan, Pagan, Alamagan), on Saipan being intermediate between this form and *saffordi*.

Meliphaga mimikae rara new subspecies

Type: AMNH No. 342965, adult male; Bernhard Camp, Idenburg River, 50 meters altitude, northwestern New Guinea; April 26, 1939; The Archbold Expedition collection.

Diagnosis: Differs strikingly from the two other known forms of this species, *granti* (type locality: Mafulu, mountains of southeastern New Guinea) and nominate *mimikae* (type locality: Mimika River, southern New Guinea) in having uniform pale yellowish grey under parts (in *mimikae* and *granti* dark grey with longitudinal yellow streaks), abdomen and flanks much paler greyish yellow, and upper parts distinctly clearer and paler green, not so brownish olive-green. Proportions, particularly tarsus, much smaller. Wing length of *rara* (adult male) 84 mm, of *mimikae* 86-88 mm, of *granti* 89-95 mm; tarsus length in *rara* 19 mm, in *mimikae* 21-22 mm, in *granti* 22-23.5 mm (only adult males measured).

Range: Only the type known.

Remarks: This form belongs to the difficult *analoga* species group. It agrees with *M. mimikae* in its general diagnostic characters (dark coloration, especially on upper parts, ochraceous under wing-coverts and pale buffish inner linings on remiges), but in other respects differs so much that it may possibly represent a separate species.

Meliphaga analoga papuae new subspecies

Type: AMNH No. 422342, adult male; Wuroi, Oriomo River, British Papua (western division), southern New Guinea; Jan. 28, 1934; The Archbold Expedition collection.

Diagnosis: Very similar to nominate *analoga* (type locality: Triton Bay, western New Guinea), but under parts distinctly paler grey with a somewhat stronger yellowish tinge; upper

parts paler, more clear greyish green, not so olive green; ear-tufts paler, yellowish white; under wing-coverts paler whitish. Proportions slightly smaller. Wing length of adult males 78-83 mm, in nominate *analoga* 81-87 (one 91) mm.

Range: Southern New Guinea from the Fly River district eastward to Hall Sound.

Meliphaga analoga connectens new subspecies

Type: AMNH No. 267966, adult male; Madang, Astrolabe Bay, northeastern New Guinea; Aug. 30, 1928; R. H. Beck collector.

Diagnosis: Differs from *flavida* (type locality: Japen Island) in having under parts paler grey with much less yellow, upper parts paler and clearer green, not so bright citrine green, and ear-tufts slightly paler yellow. Also smaller proportions than topotypical *flavida*. Differs from *stevensi* (type locality: Upper Watut River, northeastern New Guinea) by greyish white, not yellowish inner linings on remiges, paler yellow under wing-coverts, and dusky olive green, not blackish, lores and postocular spot, while the general coloration of the plumage is very similar to that of *stevensi*. Proportions slightly larger than in *stevensi*, the new subspecies in this respect forming the connecting link between *flavida* and *stevensi*. Wing length of adult males of topotypical *flavida* 82-85 mm, of *connectens* 79-83 mm, of *stevensi* 77-80.

Range: Lowlands of northern New Guinea from Wewak eastward to Huon Gulf.

Remarks: The new form comes nearest in coloration to the remote nominate *analoga* from Vogelkop Peninsula, but has the upper parts slightly clearer and paler grey; it is also smaller, and has a smaller bill.

Meliphaga versicolor vulgaris new subspecies

Type: AMNH No. 268962, adult male; Finschhafen, Huon Peninsula, northeastern New Guinea; Feb. 7, 1929; R. H. Beck collector.

Diagnosis: Similar in coloration to *sonoroides* (type locality: Waigeu Island), but much smaller. Wing length of adult males 100-108 mm, in *sonoroides* 110-114 mm. Differs from *intermedia* (type locality: Samarai Island) and nominate *versicolor* (type locality: Cape York, northern Queensland), which have similar small proportions, by the pale, whitish, not yellow under parts.

Range: Japen Island in Geelvink Bay; coastal zone of northern New Guinea from Geelvink Bay to Huon Gulf; Fergusson Island in the D'Entrecasteaux Archipelago.

Meliphaga fusca deserticola new subspecies

Type: AMNH No. 695517, adult male; Margaret River, Kimberley Division, northern Western Australia; April 20, 1902; I. T. Tunney collector.

Diagnosis: Palest of all forms within the *flavescens* group of *M. fusca*, differing from *flavescens* (type locality: Derby, northern Western Australia) by having paler grey upper parts without any brownish tinge, paler yellow under parts with very faint striation, paler yellow front and crown (and yellow color more restricted), and duller olive edges on outer web of remiges. Differs from *zanda* (type locality: Normanton, Gulf of Carpentaria) especially by the much paler grey upper parts and much duller olive edges on remiges; under parts only slightly paler.

Range: Margaret River, in arid interior of northern Western Australia.

Meliphaga penicillata interioris new subspecies

Type: AMNH No. 343828, adult male; Ward River, south of Charleville, southwestern Queensland, Australia; March 1, 1940; L. Macmillan collector.

Diagnosis: Throughout paler than nominate *penicillata* (type locality: interior of New South Wales, restricted here to Wagga-Wagga); under parts with much paler greyish throat and chest, and with whitish, not greyish, abdomen and flanks; upper parts paler and colder greyish brown, forehead and crown only slightly suffused with pale yellow, cheeks and ear-coverts yellow, without the olive greenish tinge found in nominate *penicillata;* black ear-stripe reduced or absent. Also slightly smaller. Wing length of adult males of topotypical *penicillata* 85-92 mm, of *interioris* 83-85, adult females of *penicillata* 79-83, of *interioris* 76 mm.

Range: Northwestern New South Wales, northward to south-central Queensland.

Meliphaga flaviventer tararae new subspecies

Type: AMNH No. 428247, adult male; Tarara, Wassi Kussa River, 90 miles west of Daru, British Papua (western division), southern New Guinea; Dec. 8, 1936; The Archbold Expedtition collection.

Diagnosis: Much paler throughout than *saturatior* (type locality: Aru Islands) and *giulianettii* (type locality: Aroa River, southeastern New Guinea), and, further, differing strikingly by possessing a broad and conspicuous streak of white feathers leading from gape to the white supraauricular spot. This white streak is completely missing in *giulianettii* and in the mainland populations of *saturatior,* but occasionally is present in Aru Islands birds. In *tararae* the upper throat is pale grey, lower throat and chest pale greyish brown, breast and abdomen pale buff (not rich cinnamon), flanks cinnamon (not chestnut), mantle and back distinctly paler earth-brown than in *saturatior* and *giulianettii,* and upper parts of head not so dark brown.

Range: Southern coast-land of New Guinea, between middle and lower Fly River, westward to about Digul River.

Meliphaga obscura viridifrons new subspecies

Type: Acad. Nat. Sci. Philadelphia No. 132851, adult female (labelled male); Bamoskaboe, Karoon, Tamrau Mountains, Vogelkop Peninsula, 2300 feet altitude, northwestern New Guinea; March 1, 1938; D. Ripley (Denison-Crockett South Pacific Expedition) collector.

Diagnosis: Differs from nominate *obscura* (type locality: Mt. Scratchley, southeastern New Guinea) in having front and crown green, like nape and upper parts, while in *obscura* front and crown are grey, contrasting with nape.

Range: Mountains of Vogelkop Peninsula, northwestern New Guinea. Specimens from the Weyland Mountains are intermediate between *viridifrons* and nominate *obscura.*

Melithreptus laetior normantoniensis new subspecies

Type: AMNH No. 691532, adult male; Normanton, northwestern Queensland, Australia; Jan. 31, 1914; R. Kemp collector.

Diagnosis: Differing from nominate *laetior* (type locality: Lake Eyre district, central Australia) only in its smaller proportions. Wing length of adult males 81-83 mm, in nominate *laetior* 84-90 mm; adult females 77-79 mm, in nominate *laetior* 82-84 mm.

Range: Northwestern Queensland, south of Gulf of Carpentaria. Specimens from Cooktown and Cairns area, northeastern Queensland, are probably referable to this form.

Melithreptus laetior parus new subspecies

Type: AMNH No. 691546, adult male; Exmouth Gulf, mid-Western Australia; June 21, 1902; T. Carter collector.

Diagnosis: Differing from nominate *laetior* (type locality: Lake Eyre district, central Australia) in its larger and more robust bill and, on the average, slightly longer wings. Bill length (measured from skull) in adult males 18.0, 18.5 mm, in nominate *laetior* 16-17 mm.

Range: Only known from the type locality.

Pycnopygius ixoides cinereifrons new subspecies

Type: AMNH No. 428278, adult male; two miles below junction of Black and Palmer rivers, 100 meters altitude, British Papua (western division), southern New Guinea; July 13, 1936; The Archbold Expedition collection.

Diagnosis: Differs strikingly from nominate *ixoides* (type locality: Sorong, Vogelkop Peninsula) in having grey feather edges on front, crown, and occiput, contrasting with the color of the upper parts (in *ixoides* olive green feather edges like those on upper parts); further, in having lighter brown ground color and paler olive-green feather edges on upper parts, light cinnamon throat contrasting with greyish brown breast and abdomen (in *ixoides* throat greyish brown like breast), and deeper and brighter cinnamon axillaries, under wing-coverts and inner linings on remiges, the axillaries and smaller under wing-coverts being almost bright rusty, almost as colorful as in the southeastern form *finschi*. Proportions as in nominate *ixoides*.

Range: Southern New Guinea from Mimika River eastward to upper Fly River. The population of the Weyland Mountains belongs to nominate *ixoides*, although slightly tending towards *cinereifrons*.

Philemon citreogularis carpentariae new subspecies

Type: AMNH No. 696823, adult male; Normanton, northwestern Queensland, Australia; May 1914; R. Kemp collector.

Diagnosis: In coloration, hardly differing from nominate *citreogularis* (type locality: interior of New South Wales) and *johnstoni* (type locality: Johnston River, northern Queensland), only very slightly paler generally, but differing from nominate *citreogularis* in having a much larger bill, and from *johnstoni* in having much greater wing length. Wing length of adult males:

citreogularis 136-140 mm, *carpentariae* 135-141 mm, *johnstoni* 127-131 mm; bill length: *citreogularis* 30.5-31.5 mm, *carpentariae* 33-34 mm, *johnstoni* 33-34 mm.

Range: Southern coast of Gulf of Carpentaria, northwestern Queensland.

Remarks: It is possible that the name *pseudonymus* Mathews and Neumann, 1939 (type locality: Cloncurry, northern Queensland) can be used for this form. The subspecies *pseudonymus* was based on irrelevant color characters and no measurements were given. I have seen only one specimen (adult male) from Cloncurry. It had a wing length of 130 mm, but was, unfortunately, worn, and may have measured 132 mm in fresh plumage. The bill was broken, but appeared to have been large.

Philemon novaeguineae fretensis new subspecies

Type: AMNH No. 330277, adult male; Delena, Hall Sound, British Papua (central division), New Guinea; May 28, 1929; H. Hamlin collector.

Diagnosis: Differs from nominate *novaeguineae* (type locality: Triton Bay, southwestern New Guinea), *brevipennis* (type locality: Utakwa River, southern New Guinea) and *aruensis* (type locality: Aru Islands) in being distinctly paler slate grey on upper parts and slightly paler grey on under parts, and, in addition, differs from the neighboring *brevipennis* in being much larger. Wing length of adult males: topotypical *brevipennis* 142-144 mm, *fretensis* 158 mm (same length in three specimens).

Range: Southern New Guinea from middle Fly River eastward along south coast of southeastern New Guinea to Milne Bay.

Philemon novaeguineae trivialis new subspecies

Type: AMNH No. 697135, adult male; Collingwood Bay, north coast of southeastern New Guinea; June 28, 1894; A. S. Meek collector.

Diagnosis: Same general coloration as *subtuberosus* (type locality: Fergusson Island, D'Entrecasteaux Archipelago), but slightly lighter (the *subtuberosus* from the Trobriand Islands are the darkest), with distinctly longer bill and, especially, with larger casque on bill. Length of bill in adult males of *trivialis* 47.5, 50.2 mm, in *subtuberosus* from the D'Entrecasteaux Archipelago 43-44 mm, and from the Trobriand Islands 44-47.5 mm.

Range: Northern coast of southeastern New Guinea, known from Collingwood Bay and Kumusi River.

Philemon corniculatus clamans new subspecies

Type: Los Angeles County Museum No. 15117, adult male; Wallaroo Gorge, Carnarvon Range, southeastern Queensland, Australia; July 2, 1954; K. E. Stager and J. B. Davidson collectors.

Diagnosis: Intermediate in size between the large nominate *corniculatus* (type locality: New South Wales) and the small *ellioti* (type locality: Mt. Elliot, northern Queensland). Wing length of adult males: *corniculatus* 159-166 mm, *clamans* 154-156 mm, *ellioti* 137-147 mm.

Range: Southeastern Queensland.

Melidectes fuscus gilliardi new subspecies

Type: AMNH No. 705793, adult male; Mt. Wilhelm, Bismarck Range, 11,000 feet altitude, east-central New Guinea; June 7, 1950; E. T. Gilliard collector.

Diagnosis: Same coloration as *occidentalis* (type locality: Wichmann Mountains, central New Guinea) and nominate *fuscus* (type locality: Wharton Range, southeastern New Guinea), differing from *occidentalis* in longer wing and bill, and from nominate *fuscus* in shorter bill and tarsus. The bill/tarsus ratio in the three forms is noteworthy; in *occidentalis* the bill is much shorter than the tarsus, in *gilliardi* it is equal in length with the tarsus, and in nominate *fuscus* it is longer than the tarsus. Measurements of adult males (in mm):

	WING	BILL	TARSUS
occidentalis	108-113	29.0-30.0	31.0-33.0
gilliardi	114-116	31.5-33.0	32.5-33.5
fuscus	113-117	34.0-37.0	33.0-35.0

Range: Bismarck Mountains, eastern New Guinea.

Remarks: Named after the collector, the late Dr. E. Thomas Gilliard.

Myza celebensis parvirostris new subspecies

Type: AMNH No. 300232, adult male; Mt. Tanke Salokko, 2000 meters altitude, Mengkoka Mts., southeastern Celebes; July 22, 1931; G. Heinrich collector.

Diagnosis: Differs from nominate *celebensis* (type locality: Bone Mts., Gorontalo, northern Celebes) in its much smaller proportions, especially its smaller bill. Wing length of adult males: nominate *celebensis* (from Latimodjong Mts., central Celebes) 85-87 mm, *parvirostris* 81-83 mm; bill length: nominate *celebensis* 32-34 mm, *parvirostris* 28-30 mm. No material from the type locality of *celebensis* has been examined, but a series from Ile-Ile, northern Celebes, is similar to the Latimodjong birds in measurements, although not quite so big.

Range: Mengkoka Mountains, southeastern Celebes.

PHYLIDONYRIS NOVAEHOLLANDIAE CAUDATA new subspecies

Type: AMNH No. 692106, adult male; King Island, Bass Strait, Australia; April 25, 1914; T. Tregellas collector.

Diagnosis: Differs from all other forms of this species by its distinct reduction of the yellow color in wings and tail, and by its larger proportions, particularly the longer tail. Length of tail in adult males of *caudata* 83-91 mm, compared with 75-83 mm in all other subspecies.

Range: King Island and Flinders Island in Bass Strait, Australia.

ACANTHORHYNCHUS TENUIROSTRIS TROCHILOIDES new subspecies

Type: AMNH No. 703283, adult male; Bunya Mountains, 2000 feet altitude, southeastern Queensland, Australia; Oct. 3, 1940; L. Macmillan collector.

Diagnosis: Differs from nominate *tenuirostris* (type locality: New South Wales) by having under parts (below the black pectoral band) much paler cinnamon, the band across nape dull rusty, not deep chestnut, and the mantle olive greyish green with a rusty tinge, not dark warm rusty brown; differs from *cairnsensis* (type locality: Cairns, northern Queensland) by having throat chestnut, not pale vinous pink.

Range: Restricted to the isolated pockets of rainforest in southeastern Queensland.

ACANTHORHYNCHUS TENUIROSTRIS REGIUS new subspecies

Type: AMNH No. 693497, immature male; King Island, Bass Strait, Australia; April 22, 1914; T. Tregellas collector.

Diagnosis: Only the type specimen known, an immature male, differing from all other subspecies by the very long bill, measuring 32 mm, and the extremely long tarsus, measuring 21.5 mm,

with a wing length of 71 mm. Only one other immature male has been examined, belonging to nominate *tenuirostris*, with bill 24.5 mm, tarsus 18.2 mm, wing 68 mm. The largest bill of adult birds of any subspecies is 31 mm, reached in nominate *tenuirostris;* the bill of the Tasmanian form measures in adult males 25-26.5 mm. The tarsus of adult males of the nominate form, which is the largest of all, measures 18-19 mm.

Range: King Island in Bass Strait; probably also on Flinders Island.

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A REVISION OF THE FOSSIL SELENODONT ARTIODACTYLS FROM THE MIDDLE MIOCENE THOMAS FARM, GILCHRIST COUNTY, FLORIDA

By

Vincent Joseph Maglio

INTRODUCTION

Since its discovery in 1931 the fossil locality at Thomas Farm in Gilchrist County, Florida, has proven to be the most prolific Miocene deposit east of the Mississippi River. The vertebrate fauna is impressive, both in numbers of individuals and in variety of forms present, and has greatly increased our knowledge of the Florida Miocene and its correlation with western faunas of comparable age. By far the most numerous animals are the horses, which may be used in such correlations more successfully than any other group. However, it is in the Artiodactyla that the most highly specialized forms are to be found, some of which show no close relationship to known genera of the western plains.

The strange combination of characters found in *Floridatragulus dolichanthereus,* for example, has led authors in the past to place this animal in three distinct families, the Hypertragulidae, the Protoceratidae, and the Camelidae. White (1940) described the first jaw of this species as a new genus of Hypertragulidae without discussing its relationship or similarities with other known hypertragulids. Additional specimens (referred to this species in the present paper) were subsequently named as a second species of *Floridatragulus* (White, 1947), a second genus of Hypertragulidae, *Hypermekops olseni* (White, 1942), and, in the case of a partial palate, as a species of *Syndyoceras,* a protoceratid (White, 1941). Following White's determinations, Romer (1947) retained these generic names in his discussion of the mammalian fauna of Thomas Farm. It was not until 1957, when Professor Bryan Patterson prepared a manuscript catalogue of the Thomas Farm vertebrates in

the collections of the Museum of Comparative Zoology, that a major reorganization of the taxa became available. In this reference, Patterson considered all of the above specimens as a single camelid species. Although never published, this list has become incorporated, partially or completely, into almost every major taxonomic reference concerning late Tertiary Floridian mammals, most notably Ray, 1957, and Puri and Vernon, 1964.

A similarly confused story is associated with the history of *Nothokemas floridanus,* which was originally made the nominate genus of a new hypertraguloid family, the Nothokemadidae (White, 1947). This, also, was referred to the Camelidae by Patterson.

No new material has been added to the MCZ collection since 1957, but it became clear that a restudy of these artiodactyls in the light of Patterson's list was necessary. This is the purpose of the present work, which, in addition, presents a more detailed description of the species involved than has hitherto been available. A concurrent study of the postcranial remains has contributed to our knowledge of these forms.

The present study confirms Patterson's findings except for the change in rank of *Synthetoceras australis* and the interesting addition of an oreodont to the fauna.

A discussion of the perplexing geological problems involving the bone-bearing sediments of the Thomas Farm is beyond the purpose and scope of this report, but a detailed review is available in Puri and Vernon (1964). Older accounts of the quarry itself may be found in Simpson (1932), and White (1942).

I am indebted to Professor Bryan Patterson for suggesting the problem and for his helpful discussions and suggestions throughout the course of the research. I also wish to thank Dr. Malcolm McKenna for permitting the examination and loan of specimens in the American Museum and Frick collections. Mr. Morris F. Skinner for his help in the identification of the oreodont remains, and Mr. Beryl E. Taylor for his examination of some indeterminate camel molars.

Abbreviations used in this paper are as follows: American Museum of Natural History (AMNH), Carnegie Museum (CM), Florida State Geological Survey (FSGS), Museum of Comparative Zoology (MCZ), and Yale Peabody Museum (YPM).

DESCRIPTION OF SPECIES

CAMELIDAE

FLORIDATRAGULINAE new subfamily[1]

FLORIDATRAGULUS DOLICHANTHEREUS White

Floridatragulus dolichanthereus White, 1940, p. 35, pl. VII.
Syndyoceras australis White, 1941 (in part), p. 97, pl. XV, figs. 1a, 1b.
Hypermekops olseni White, 1942, pp. 11-12, pl. 8.
Floridatragulus barbouri White, 1947, pp. 505-507, fig. 4.

Hypodigm: MCZ 3635, type, incomplete mandible with M_1 to M_3 and alveoli for P_1 to P_3, anterior crescent of right M_1 and hypoconulid of right M_3 missing, both ascending rami and the symphysis anterior to the C-P_1 diastema missing; MCZ 4086 (type of *F. barbouri*), right mandible with partial symphysis and complete ascending ramus, left canine, right P_2 to M_3 and the alveoli for P_1; MCZ 3711 (type of *Hypermekops olseni*), incomplete skull with right I^1 and I^2, P^4 to M^3, left I^2, P^4 to M^3, and the alveoli for the remainder of the dentition; MCZ 3642 (paratype of *Syndyoceras australis*), left palate with P^3 to M^3; MCZ 4291, right mandible with P_3 to M_3 and alveoli for P_1 and P_2; MCZ 7780, 30 astragali; MCZ 7781, 11 calcanea; MCZ 7782, 15 cuboids; MCZ 7783, 11 naviculars; MCZ 7784, 41 proximal phalanges; MCZ 7785, 10 second phalanges; MCZ 7786, 6 ungual phalanges; MCZ 7787, 4 metapodials.

Horizon and locality: Middle Miocene, Hawthorne Formation, Thomas Farm, 8 miles north of the town of Bell, Gilchrist County, Florida.

Redescription: The referred skull (MCZ 3711) is a reconstruction of a badly broken and incomplete specimen designated as the type of the supposed hypertragulid, *Hypermekops olseni,* by White (1942, pl. 8). Its most striking character is the narrow and very long snout, the region from P^2 to the anterior tip of the premaxillary being more than twice the length of the continuous premolar-molar series. The anterior teeth from I^1 nearly to P^2 form straight rows on each side of the snout, parallel to each other. Just anterior to P^2 the palate begins to widen, becoming, at the level of M^3, more than twice the snout width. The skull is very low throughout, with the nasal bones nearly parallel to the palate below. Above, the frontals are expanded and send down broad, flat, postorbital processes which do not reach the zygomatic arch, the orbit being open behind. The cranium is largely missing, but

[1] See page 9 for diagnosis.

parts of the occipital and temporal regions are preserved. The supraoccipital forms a very high lambdoidal crest, considerably higher than in *Paratylopus primaevus* and more vertical in orientation. Although the parietals are missing, there are indications that the sagittal crest was also quite prominent. The occipital condyles are relatively narrower than in *Paratylopus primaevus;* these are confluent in MCZ 7764 but separated by a median groove in MCZ 3711. The auditory region is poorly known, only the posterolateral portion of the right bulla being present. It is clear that this fragment was erroneously oriented on the reconstructed skull and was almost certainly closer to the condyles, with the tympanohyal recess and groove directed posterolaterally rather than laterally, as restored. The bullae were also probably somewhat larger than figured and filled with spongy bone. The molar series is situated well forward, with the posterior edge of M^3 some distance in front of the orbit; the internal nares open behind this tooth.

The lower jaw of *F. dolichanthereus* shows many specializations similar to those of the skull, especially in the great elongation and in the reduction of the premolars. The mandible is narrow anterior to P_1 and expands to approximately five and a half times that width at the angle of the jaw. The symphysis is long, ending some distance behind P_1, with the jaws solidly fused along its length. The angle of the jaw is strongly hooked in typical camelid fashion, and the coronoid process is long and narrow. The jaw is very deep posterior to P_2, as in *Myotylopus bathygnathus.*

The dental formula is $I\frac{3}{?}$, $C\frac{1}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$. In MCZ 3711 I^1 is a large, caniniform tooth worn posteriorly along its entire height and along a broader area lingually. It is situated on the side of the snout near the posterior margin of the elongated incisive foramen.

A long diastema separates I^1 and I^2; this is the longest spacing within the dental row. I^2 is also caniniform, smaller than I^1 and somewhat compressed laterally. Its anterior and posterior margins are raised to form a blade-like ridge. It is strongly recurved, and except for a small area at the very tip, is unworn.

I^3 is separated from I^2 by a diastema equal to somewhat less than half that separating the first two incisors. This tooth is missing on both sides but the alveoli indicate a tooth similar to, but smaller than I^2. The alveolus for the canine follows after a very short diastema equal to little more than its own diameter, and suggests a tooth no larger (and probably smaller) than I^3. After another equally short diastema comes the alveolus for P^1. This

was a single-rooted tooth and could not have been more than a mere vestige judging from the size of the socket.

A very long diastema nearly equal to that separating I^1 and I^2 separates P^1 and P^2. The second premolar (Fig. 1) is a long, narrow, two-rooted tooth similar to that in *Poebrotherium wilsoni* and in its relation to the molars it is essentially unreduced from the condition in that species. Its three cusps are in a straight line and are connected to each other by a sharp, high ridge. A weak basal cingulum is present along the anterior and posterior of the lingual surface and a well developed parastyle runs the height of the tooth.

P^3 is preserved on the referred palate, MCZ 3642, and is only slightly reduced, three cusped, and three rooted. It is shorter and wider than P^2 with the internal basal cingulum similarly developed, but less so than in *Poebrotherium*. Externally, the tooth is simple with the parastyle nearly indistinguishable and the mesostyle represented only by a low convex ridge.

The fourth premolar is a small triangular tooth with a shorter inner crescent that remains separate from the outer crescent until the tooth is considerably worn. The difference in length between the inner and outer crescents is about as in *Paratylopus primaevus* and, as in that species, the inner crescent is skewed anteriorly. The outer face is relatively simple with low antero- and postero-external styles and a low median convex ridge. Short weak cingula are present on the anterior and posterior sides of the inner crescent. This tooth is somewhat more reduced than in *Oxydactylus longipes* or *Paratylopus primaevus,* which are more nearly like *Poebrotherium* in this respect.

The molars increase in both length and width from M^1 to M^3, as in *Paratylopus primaevus,* and are as brachyodont as in that species. M^1 is wider than it is long resembling the nearly square first molar of *P. primaevus* and *M. bathygnathus,* more so than the elongated M^1 of *O. longipes.* This tooth is only moderately worn in MCZ 3642 and has a strong parastyle, as in *"Paratylopus" cameloides.*[2] The mesostyle is directed perpendicular to the outer face of the tooth and is as strong as in *O. longipes.* The metastyle is absent. The median ridges on the outer face of the tooth are very prominent, especially on the anterior crescent, and widen somewhat near the base of the crown. This last feature is similar to the condition found in *P. primaevus* and quite unlike that in

[2] I am not convinced that *cameloides* belongs in this genus.

Poebrotherium or *Oxydactylus*. A prominent internal pillar rises from the bases of the protocone and hypocone, particularly the latter. A similar pillar is found in *M. bathygnathus* and *"P." cameloides* and incipiently on M^3 of *P. primaevus*. The protocone remains separated from the mesostylar region until worn nearly to the base of the crown, whereas the hypocone fuses to this area somewhat earlier. A very weak basal cingulum marks the posterior edge of the hypocone.

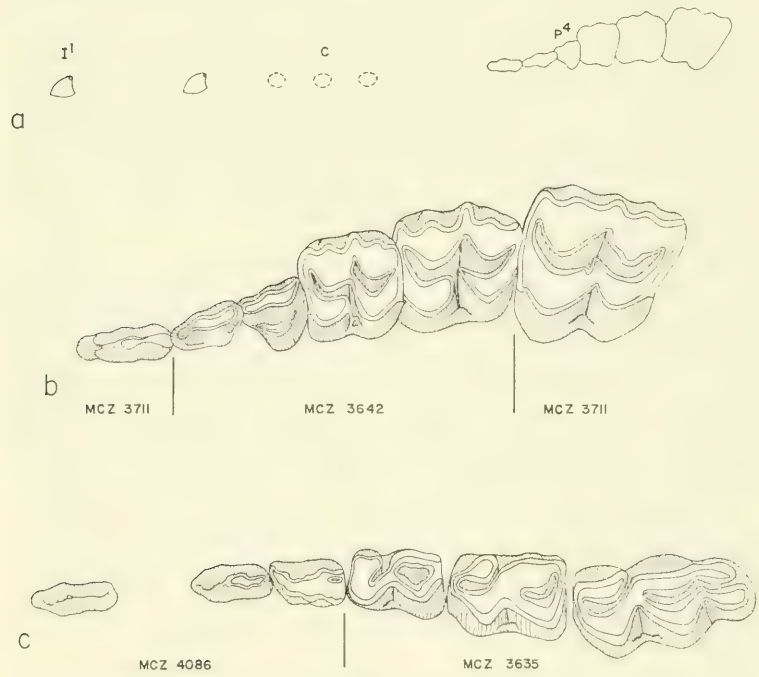

Figure 1. *Floridatragulus dolichanthereus*. *a*, Diagram of upper dentition, X 4/5. *b*, *c*, Composite crown view of left cheek teeth; *b*, upper P^2 to M^3, *c*, lower P_2 to M_3, X1.

M^2 is as long as it is wide in MCZ 3642, but slightly wider than long in MCZ 3711. It is similar to M^1 with the para- and mesostyle more prominent. The median ridge of the anterior crescent is considerably stronger than that of the posterior one. M^3 is similar to M^2, but with a somewhat weaker and less compressed mesostyle.

The lower incisors are unknown. A large, strongly recurved canine is present in MCZ 4086 and is heavily worn posteriorly to a point below the crown. The tooth is slightly compressed laterally and emerges from its socket at a lateral inclination of about 20 degrees from the vertical.

P_1 is separated from the canine by a long diastema somewhat exceeding the combined length of M_1 and M_2 in the type, but variable in referred specimens. P_1 is not preserved, but the alveoli indicate a small, one-rooted tooth probably similar to P^1 and roughly equivalent to it in size.

After another long diastema the second premolar follows (Fig. 1c) and is a simple, two-rooted, three-cusped, trenchant, and laterally compressed tooth. The cusps are essentially in a straight line, the anterior cusp being very slightly inflected medially as in *Poebrotherium eximium,* but the tooth is generally much more robust than in that species. This tooth did not occlude with the upper dentition, as shown by its completely unworn condition.

The diastema between P_2 and P_3 is quite variable; that of MCZ 4086 is 52 per cent smaller than that of the type. P_3 is similar to P_2 but more robust. The anterior cusp is more inflected producing a well defined parastylid which does not continue to the base of the crown. Only a suggestion of a posterior intermediate crest is present internal to the median cusp. The outer surface is simple and gently convex.

P_4 follows immediately behind P_3 and is shorter and broader than the latter. This tooth strongly contrasts with its homologue in *O. longipes,* being somewhat more reduced and morphologically simplified. The anterior cusp is more inflected than in P_3, but does not form the prominent right angle of *Poebrotherium wilsoni,* nor the sharply bent and somewhat expanded anterior column of *Oxydactylus.* The lake enclosed between the posterior and posterior intermediate crests is relatively small and shallow. Laterally the surface is simple, lacking prominent ridges and troughs.

The molars become larger from front to back, are simple and generally similar to each other. The lingual faces of the inner crescents are gently convex and for the most part lack distinct stylids and median ridges. A parastylid is only suggested on the type, but is absent on MCZ 4291, and present, although weak, on MCZ 4086. A distinct median pillar rises from the bases of the external crescents of each molar.

The metaconid remains isolated from the other crescents until worn to the base, whereas the anterior crest of the hypoconid fuses

early to the entoconid and protoconid. The hypoconulid is divided, forming two grinding surfaces; the space between these is continuous with the space between the posterior pair of crescents in young individuals. The two grinding surfaces quickly fuse at their anterior extremity and the fusion proceeds posteriorly with wear.

Discussion: From the material available, it appears that only one species of *Floridatragulus* is represented in the Thomas Farm fauna. As mentioned above, the P_1-P_2 and P_2-P_3 diastemata are quite variable, but this may be due to the functionless condition of P_2. Similar variation is observed in *Lama* with respect to the non-occluding canine. The referred jaw, MCZ 4291, is not as deep as in the type or in MCZ 4086 by about 30 per cent. This kind of variation is also seen in *Lama*, although not to the same extent. MCZ 4291 also differs in the position of the posterior extent of the symphysis which is almost directly under P_1 rather than about 14 mm behind this tooth as in the type. McKenna (1966) notes two species of *Floridatragulus*, but does not discuss the reasons for this decision. The differences noted above possibly indicate a second species, but until additional material is available for study it is preferable to refer this specimen (MCZ 4291), at least tentatively, to *F. dolichanthereus*.

The camelid affinities of this species are inferred from such typical characters as the hooked angle of the jaw, auditory bullae filled with spongy bone and divided by a tympanohyal pit and groove, relatively simple premolars, and the similarity of the dentition as a whole to those of such early camels as *Poebrotherium* and *Paratylopus*.[3]

The upper dentition of *F. dolichanthereus* is more nearly like that of *Paratylopus primaevus* than like the Miocene *Oxydactylus*-like camels. The open orbit, squared molars, retention of prominent mesostyles, presence of median internal pillars, and graded increase in size from M^1 to M^3 indicate an origin close to *P. primaevus*. In the elongated snout and deep jaws this form resembles *Miotylopus bathygnathus*, but this similarity is probably no more than a parallel development of habitus characters. Other characters which *Miotylopus* shares with *Floridatragulus*, such as median pillars, reduced upper canine, and (probably) an open

[3] G. M. Allen, in a personal communication to T. Barbour, expressed this view more than 20 years ago (correspondence in the Harvard Archives).

orbit, more likely indicate retention and development of the primitive characters of a *Paratylopus*-like ancestor than any close phylogenetic relationship.

The many distinctive characters which separate this genus from other late Tertiary Camelidae have justifiably confused past workers. The greatly elongated snout is a peculiar habitus character, which is only distantly approached in such specialized forms as *O. longirostris* and *"P." cameloides,* and the large caniniform incisors decreasing in size from I^1 to I^3 are peculiar to this genus. In the mandible the long symphysis and exceptionally narrow jaw strongly divergent in the region of the cheek teeth are not seen in other camels. Also, the very simplified premolars and divided hypoconulid of M_3 tend to set this form off from other Miocene camels.

A number of astragali, calcanea, and proximal phalanges are referred to this species. The tarsal bones are similar to those of other Miocene camels and show no distinctive characters. As is common in other camels with an elongated snout, the phalanges are long and slender.

Two distinct morphological groups of phalanges are present; these are differentiated by the symmetry and dorsal extent of the distal articular facet. Differences of this type are present between the manus and pes of the Recent species of *Dorcatherium, Moschus,* and *Lama* and probably represent manus-pes differences in the present species also.

The referred metapodial fragments show that the metatarsals are closely appressed, with some fusion near the proximal end; the plantar processes are completely coossified. Metatarsal II is fused with metatarsal III, whereas metatarsal V is entirely separate from metatarsal IV and articulates with it by a small facet. Metacarpals III and IV are separate.

Because of the very peculiar characters of this genus and because of its distant relationship to contemporary camelids, it is proposed that a new subfamily, the Floridatragulinae, be established to receive it, with the subfamilial diagnostic characters being those of the genus until such time as additional members of this group are found.

Diagnosis of the Subfamily Floridatragulinae

Differing from Miocene Alticamelinae in retention of many primitive characters such as complete brachyodont dentition, open orbits, and nearly square upper molars with median pillars; upper

incisors caniniform, lateral in position, separated from each other by diastemata, unlike those of Camelinae; premolars tending toward reduction and simplification, but less so than in Stenomylinae; lower molars simple with pillars, hypoconulid of M_3 divided.

TABLE 1

Comparative measurements of *Floridatragulus dolichanthereus* in mm

	Floridatragulus dolichanthereus		*Paratylopus primaevus*
	MCZ 3711	MCZ 3642	AMNH 9806
Skull length to condyles	[a]385	—	[a]200
Width of palate at P^1	45	—	21
Width of palate at M^2	[a]76	—	52
Ratio: snout (Pmx to orbit) to skull length	[a]0.70	—	0.51
Tip of Pmx to I^1	23	—	—
I^1 length	9	—	—
I^1 width	7	—	—
I^2 length	7	—	—
I^2 width	4.5	—	—
I^1 to I^2 diastema	37.5	—	—
I^3 to canine	9	—	3
Canine to P^1 diastema	9	—	4
P^1 to P^2 diastema	28	—	7.5
P^1 length	11.5	—	—
P^1 width	4	—	—
P^3 length	—	10	—
P^3 width	—	5	—
P^4 length	9	9	8
P^4 width	8.5	8.5	[a]8
M^1 length	[b]12	13.5	[a]10
M^1 width	[b]15	15	[a]12
M^2 length	16	17	[a]13
M^2 width	17	17	[a]13
M^3 length	18.5	—	16
M^3 width	18.5	—	14.5

	Floridatragulus dolichanthereus		
	MCZ 3635	MCZ 4086	MCZ 4291
Jaw length	—	[a]300	—
Length of symphysis behind P_1	13	14	3
Width of jaw at P_1	18.7	19.5	—
Width at M_3	—	[a]70	—
Depth of jaw under P_1	21.5	21	14
Depth under P_4	[a]32	32	23
Depth under M_3	[a]38	37	[a]32?
Canine to P_1 diastema	—	28.5	—
P_1 to P_2 diastema	33	37	24
P_2 length	—	10.5	—
P_2 width	—	3.7	—
P_2 to P_3 diastema	21	10.5	19.5
P_3 length	—	10.5	[a]10.5
P_3 width	—	4.5	[a]4.5
P_4 length	—	10	[a]10
P_4 width	—	6	6
M_1 length	[a]13	10	10.5
M_1 width	[a]9	9	8.5
M_2 length	15.5	15	15.5
M_2 width	11	11	11
M_3 length	25.5	13	13
M_3 width	12.5	13	13

[a] estimate based on incomplete specimen.
[b] worn.

ALTICAMELINAE

Nothokemas floridanus (Simpson) 1932

Oxydactylus floridanus Simpson, 1932, pp. 35-37, figs. 20, 21.
Paratylopus grandis White, 1940, p. 33, pl. V.
Nothokemas grandis White, 1947, pp. 508-515, figs. 5, 6.

Hypodigm: FSGS V-5247, type, incomplete right maxilla with P^2 to M^3; FSGS V-5238, paratype, right lower jaw with P_3 to M_3; MCZ 3636 (type of *N. grandis*), incomplete right mandible with P_3 to M_3 and alveolus for P_2; MCZ 4322, right maxilla with P_2 to M_3; MCZ 4323, left mandible with P_4 to M_2 and anterior crescent pair of M_3; MCZ 4324, partial left mandible with P_2 to

P_4; MCZ 4325, left mandible with M_1 to M_3 and alveoli for P_2 to P_4; MCZ 4326, left mandible with dP_3 to M_2; MCZ 4329, crushed skull with poorly preserved P^2 to M^3, rostrum anterior to P^1-P^2 diastema missing; MCZ 4541, crushed skull with dP^2 to M^3, anterior snout missing; MCZ 7297, left mandible with dP_4 to M_3; MCZ 7592, incomplete left mandible with M_2 to M_3; AMNH 22672, left mandible with P_2 to M_3; MCZ 7767, 22 astragali; MCZ 7768, 10 calcanea; MCZ 7769, 17 cuboids; MCZ 7770, 3 naviculars; MCZ 7771, 15 proximal phalanges; MCZ 7772, 23 second phalanges; MCZ 7773, 8 ungual phalanges.

Horizon and locality: Middle Miocene, Hawthorne Formation, Thomas Farm, Gilchrist County, Florida.

Redescription: The present description is based on Simpson's account (1932, pp. 35-37) and on the referred material in the Museum of Comparative Zoology and American Museum of Natural History collections.

This species is about the size of *Oxydactylus brachyodontus* Peterson 1904 in measurements of the dentition, but the maximum skull length was doubtless considerably greater due to the elongation of certain of the diastemata. The rostrum is deep and very narrow. A prominent, quadrangular lacrimal vacuity lies in the maxillary bone and is as large as the orbit. The latter is completely closed behind by a wide process from the frontal bone. The last molar is somewhat anterior to the orbit, but less so than in *Floridatragulus.*

The incisors and canine are unknown; the anterior portion of the snout is missing on both referred skulls. A small depression is present in some broken bone on the anterior edge of MCZ 4329 which may be the socket for P^1. If this is correct this tooth was single rooted as in *O. brachyodontus,* but was very much smaller, being only a tiny and almost certainly functionless vestige. Behind P^1 is a long diastema approximately equal to the combined lengths of P^4, M^1 and M^2.

P^2 is a long, narrow, trenchant tooth essentially unreduced. Proportionately, it is narrower than in *O. longipes,* being more similar in this respect to *O. longirostris.* A complete internal basal cingulum originates anteriorly at the base of a style. A similar anterior style is present on the external face. The external and internal surfaces are somewhat folded and expanded into a convex longitudinal ridge in the region of the median cusp. The posterior cusp is strongly skewed externally in MCZ 4329, but less so in 4322.

P^3 is larger than P^2, considerably wider, and has a much stronger internal cingulum. A strong parastyle forms a wide convex fold and is continuous around the front of the tooth with a very narrow anterointernal style.

P^4 has the internal crescent fully expanded and somewhat skewed anteriorly, as in *"Paratylopus" cameloides*. It is nearly as wide as it is long, resembling in this respect *"P." cameloides* and *O. longirostris* rather than *O. longipes*. A well developed cingulum extends along the posterior base of the internal crescent and a weaker one is present on the anterior side. The external surface is ribbed by a prominent anterior style, which widens toward the base, and a variable posterior style, which is moderately developed on MCZ 4329, but nearly absent on MCZ 4322.

The upper molars are brachyodont, with M^2 the widest of the series, as in *O. longipes*. They are proportionately longer and wider than in *"P." cameloides* and resemble *O. longipes* more than any other species in this respect. A prominent internal pillar, V-shaped in cross-section, is present on all the molars, but decreases in size from M^1 to M^3. In this character *Nothokemas* resembles *"P." cameloides* and contrasts with the pillarless molars of *Oxydactylus*.

M^1 has a moderate parastyle and strong mesostyle, the latter directed somewhat anteriorly. The metastyle is very weak to absent and the median ridges of the external faces are prominent, especially on the metacone. A strong basal cingulum extends around the base of the protocone becoming weak to nearly absent on the most lingual part of the crescent. A similar crescent is present along the posterior edge of the hypocone. The internal crescents remain separated from the outer ones until an advanced stage of wear is reached.

M^2 is similar to M^1, but is longer and has more prominent styles and ridges. The basal cingula are generally weaker and less extensive around the lingual curves. M^3 is proportionately more elongated than M^2, the styles more prominent, and the cingula nearly absent. In contrast to *O. longipes* the parastyle is weak as in *"P." cameloides*. Also as in *cameloides* the protocone is somewhat narrower anteroposteriorly than the hypocone.

The mandible is long and relatively shallow as compared with that of *O. longipes*. The anterior portion of the symphysis, from I_1 to P_1, is unknown. MCZ 4325 has a broken symphyseal area which contains what may be the socket for P_1. If it is, this tooth was only slightly larger than P^1 and situated well in front of the posterior border of the symphysis. The long diastema between P_1

and P_2 is comparable to that in the upper dentition, being at least 43 mm in length in MCZ 4325.

The premolars are large and unreduced, and increase in size from front to back. P_2 is expanded medially with its internal face strongly convex. A small anterior cusp is connected with a high and pointed median cusp by a blade-like anterior crest. The posterior crest is strongly deflected laterally before turning posterad so that the posterior cusp lies external to the straight line through the anterior and median cusps. A strong posterior intermediate crest extends back from the central cusp for about one-half the distance to the posterior margin of the tooth, forming a shallow open valley between itself and the posterior crest.

P_3 has the anterior cusp very strongly inflected internally, more so than P_4. The posterior intermediate crest is somewhat more developed than in P_2, enclosing with the posterior crest a deeper but still medially open valley. P_4 is similar to P_3, but with the posterior intermediate crest long and completely enclosing a deep valley, which is confined to the posterior one-third of the tooth. A well defined cusp is present on the crest near its posterior margin, and a slightly oblique longitudinal ridge extends along the length of the crown on the lingual surface.

The lower molars are long and narrow, as in *O. brachyodontus* and less so than in *O. longipes*. A strong median pillar, variable in size, rises primarily from the protoconid, at least on M_2. The metaconid remains isolated to the base and somewhat overlaps the entoconid, whereas the latter fuses with the protoconid early in wear. The entoconid overlaps the hypoconulid for about one-fourth of the latter's length and remains separated from it nearly to the base of the crown. A very weak parastylid is present on M_2.

The tarsal bones and phalanges that may be referred to *Nothokemas* on the basis of size and relative abundance are very *Oxydactylus*-like, and the cuboid and navicular are separated, unlike those of hypertragulids. It is surprising that the limb material does not show the stilt-like character that might be expected to be associated with the elongated snout. These elements are somewhat more slender than those of *O. longipes,* but not nearly as stilt-like as in *O. longirostris.*

Discussion: Nothokemas floridanus differs from the hypertragulids, to which it was first referred (White, 1947), principally in the structure of the premolars, but also in that of the molars. In *Hypertragulus,* P_3 is a simple, single-rooted tooth with a very weak posterointernal fold, while the comparable tooth in *Nothokemas* is three cusped and much more complex in its folds and

TABLE 2

Comparative measurements of *Nothokemas floridanus* in mm

	Nothokemas floridanus			*Oxydactylus longipes*	*"Paratylopus" cameloides*
	MCZ 4329	MCZ 4322	MCZ 4541	CM 918	YPM 10917
Skull length	[a]340	—	—	340	[b]278
P^1-P^2 diastema	[a]53	—	—	18	—
P^2 length	13	12.5	—	11	—
P^2 width	6	5.2	—	6	—
P^3 length	[a]13.3	13.4	—	14	—
P^3 width	8.5	7.5	—	8	—
P^4 length	[a]13	13	—	14	11
P^4 width	11	12	—	10	10
M^1 length	—	18.6	19.7	19	13
M^1 width	—	18.5	18.5	16	—
M^2 length	—	[a]22	22	23	17.3
M^2 width	—	21.5	20.5	20	16.5
M^3 length	23	23	23	25	17.4
M^3 width	19	19.5	18.8	20	17.3

	Nothokemas floridanus			*Oxydactylus longipes*	*"Paratylopus" cameloides*
	MCZ 3636	MCZ 4325	MCZ 4324	CM 918	AMNH 8197
P_1-P_2 diastema	—	45.5	—	17	21
P_2 length	—	—	10.8	10	10
P_2 width	—	—	4.5	5	—
P_3 length	13.8	—	12.8	12	12.5
P_3 width	6.4	—	5.5	5	4.3
P_4 length	15	—	14.5	12	13
P_4 width	7.5	—	7.3	7	5.9
M_1 length	[a]18	19.2	—	18	14
M_1 width	10.7	10.7	—	10	14
M_2 length	21.5	23.6	—	23	17.5
M_2 width	14	13.2	—	14	11
M_3 length	35	33	—	31	25
M_3 width	16.5	14.1	—	13	12

[a] estimated from incomplete specimen.
[b] estimated from figure, Dougherty, 1940.

crests. P_4 is marked by a very strongly inflected parastylid in *Hypisodus* and *Hypertragulus,* more prominent than in *Nothokemas* and extending farther towards the base of the crown. A strong stylid extends along the internal surface of the median cusp in the above mentioned hypertragulids so that the depression formed in front and behind this is very much deeper in the Florida species.

The lower molars of *Hypertragulus* are complicated by very strong cingula and strong pillars rising primarily from the protoconid. In hypertragulids generally, the hypoconulid is strongly divided, a condition not seen in *Nothokemas.* The upper dentition is also quite different, and generally more complex in the Hypertragulidae.

There can be no question that the dentition as described above is indicative of camelid affinities, a conclusion supported by the referred postcranial elements. Although highly specialized, *Nothokemas floridanus* presents no characters which could not easily be derived from an early *Oxydactylus*-like form, from which *"P." cameloides* may also have arisen. In many of its characters *Nothokemas* stands somewhere intermediate between typical *Oxydactylus* (as represented by *longipes* and *brachyodontus*), on the one hand, and *"P." cameloides,* on the other, and it is likely that both *N. floridanus* and *"P." cameloides* represent early specialized offshoots from the basal *Oxydactylus* line that possibly arose in earliest Arikareean time.

Camelidae gen. et sp. indet.

Several isolated teeth and bones suggest the presence of a third camelid in the Thomas Farm fauna. Three upper molars, MCZ 7811, are generally comparable to those of *Oxydactylus* from the Marsland deposits of western Nebraska and eastern Wyoming, but are higher crowned (Beryl Taylor, personal communication). P^3 is represented by two specimens, MCZ 7812, which are very similar to P^3 of *Alticamelus* in structure, but are considerably narrower. Four proximal phalanges, MCZ 7813, are long and slender with ungrooved distal articular facets and a very shallow proximal surface.

All of these specimens suggest the presence of a camel of a somewhat more advanced type than *Floridatragulus* or *Nothokemas,* but only additional material will reveal its relationships.

PROTOCERATIDAE

SYNTHETOCERAS (PROSYNTHETOCERAS) RILEYI AUSTRALIS (White), 1941 new rank as subspecies

Syndyoceras australis White, 1941 (in part), p. 97, pl. XV, figs. 2, 2a.
Synthetoceras (Prosynthetoceras) douglasi White, 1947, pp. 504-505, fig. 3a.

Hypodigm: MCZ 3654, type, right mandible with P_1, P_4 to M_3, and alveoli for P_2 and P_3, coronoid process and symphysis anterior to P_1 missing; MCZ 3708, right mandible with P_3 to M_3 and alveoli for I_1 to P_2; MCZ 3655, right mandible with P_1 to M_3 and partial alveoli for I_2 to the canine; MCZ 3656, right mandible with P_1 to M_3 and partial alveoli for I_2 to the canine; MCZ 3666, partial right mandible with P_3 to M_3; MCZ 4065 (type of *Synthetoceras douglasi*), palate with right and left P^3 to M^3; MCZ 7635, right mandible with P_4 to M_3 and alveoli for I_2 to P_3; MCZ 7636, incomplete left mandible with P_4 to M_3; MCZ 7637, left mandible with P_3 to M_3 and alveoli for P_1 and P_2; MCZ 7774, 13 astragali; MCZ 7775, 3 cuboids; MCZ 7776, 4 naviculars; MCZ 7777, 22 proximal phalanges; MCZ 7778, 19 second phalanges; MCZ 7779, 5 ungual phalanges.

Horizon and locality: Middle Miocene, Hawthorne Formation, Thomas Farm, 8 miles north of the town of Bell, Gilchrist County, Florida.

Diagnosis: Equal in size to *Synthetoceras rileyi rileyi*[4] Frick, but P_3 is 13 per cent smaller, and median cusp of P_4 somewhat narrower, so that internal depression is flatter and deeper.

Description: The mandible is long and slender, remaining rather shallow beneath the molars. The angle of the jaw is a smooth, continuous curve, as in *Protoceras*. Anterior to P_2, the jaw begins to flare outward so that P_1 is inclined at about 35 degrees from the vertical.

The alveoli for the incisors indicate that they were small, closely spaced, and quite procumbent. That for the canine is larger and also procumbent and close behind I_3, suggesting that it was a functional member of the incisor series, as in *Protoceras*. P_1 follows after a short diastema equal to M_1 in length. In the

[4] Frick's collection data is not precise, but the type specimen appears to have been collected in the Catahoula sandstone in Walker County, Texas. Although the age of this formation is still not settled, Fisk (1940) considers it of Miocene age, and Gidley (see Renick, 1936) of Middle Miocene age.

type and MCZ 3656 and 7637, P_1 is a large, single-rooted, recurved, caniniform tooth laterally compressed and with blade-like anterior and posterior edges. In MCZ 3708, 7635, and 3655 the alveolus for the first premolar indicates a very tiny vestigial tooth which could not have been functional to any great extent in the living animal. In size and dental morphology these two groups are identical. Since dimorphs of this kind are known among artiodactyls, and with no evidence to the contrary, it is preferable to consider these as sexual morphs rather than two distinct taxa, the latter group being the females.

A long diastema separates P_1 and P_2. The latter is a two-rooted, simple, robust tooth equal to P_3 in length (Fig. 2). P_3 is proportionately smaller than the corresponding tooth in *S. rileyi rileyi,* but similar to it in structure. The anterior edge is somewhat recurved onto the internal face forming a moderate stylid. The high median cusp is connected with the anterior and posterior cusps by narrow crests. A posterior intermediate crest extends backward nearly to the edge of the tooth, but fails to fuse with the posterior crest, resulting in a partially closed lake which is open posteromedially.

P_4 is similar to P_3 with a stronger parastylid and a lake which is completely closed near the base of the crown. It differs from *S. rileyi rileyi* in having a narrower median cusp.

The molars are indistinguishable from those of *S. r. rileyi.* M_1 and M_2 have narrow crescents, strong parastylids, and weak metastylids. The median ridges are well developed, especially on M_2. M_3 is similar but with the posterior edge of the metaconid slightly overlapping the entoconid. The hypoconulid is C-shaped forming two functional grinding surfaces, and is quite variable in size.

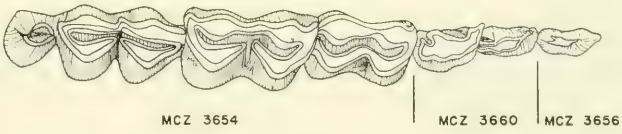

Figure 2. *Synthetoceras* (*Prosynthetoceras*) *rileyi australis,* composite crown view of right lower cheek teeth, X1.

In the upper dentition, the referred palate most closely resembles that of *Synthetoceras francisi* Frick. M^3 is longer than broad with the posterior pair of crescents narrower than the anterior pair. The metastyle is weak and the mesostyle prominent, but less so

than in *S. francisi.* The parastyle is as strong as the mesostyle. The internal crescents fuse early and extend as a narrow process between the external crescents, which they do not fuse with until late in wear. A median pillar, check-shaped in cross section, is present between the internal crescents, with the longer arm along the protocone. A prominent elongate pillar rises from the cingulum along the anterior side of the protocone.

M^2 is smaller than M^3 and shorter anteroposteriorly than in *Synthetoceras tricornatus;* the styles are as prominent as in that species and the median ridges are low and indistinct. M^1 is the smallest of the molar series and, although worn, appears to be similar to M^2 in character.

P^4 is triangular, as in *S. francisi,* with a very strong anteriorly curved metastyle. Unlike conditions in the corresponding tooth of that species, however, the parastyle is nearly absent. P^3 resembles that of *S. francisi,* but has a stronger metastyle and a strong and complete internal cingulum. A small wear facet on the anterior edge of P^3 indicates that P^2 was present, as in *S. francisi.*

On the basis of relative size, a number of foot bones are referred to this species. The phalanges are short and heavy as in *Protoceras.*

Discussion: As can be seen from Table 3 the range of variability of *S. australis* is sufficient to include the type of *S. rileyi.* In the character of the molars there are no differences which could not be attributed to intraspecific variation. The premolars, except for the differences already noted, are nearly identical in the two forms.

The subspecific rank of *S. rileyi australis* is proposed in view of the premolar differences, and the distance between Walker County, Texas, and Gilchrist County, Florida (nearly 800 miles), and because of the possibility of a slight difference in horizon between these localities. Since both forms are so poorly known at present it is advisable to retain a subspecific distinction, at least until the extent of variation in each is better known.

Frick (1937) was apparently uncertain as to the subgeneric reference of *S. rileyi,* questionably placing it in the subgenus *Synthetoceras.* The subgeneric distinction between *S. (Synthetoceras) tricornatus* and *S. (Prosynthetoceras) francisi* is based on the smaller size of the latter, its shorter crowned teeth, the retention of P^2, and the prominence of the upper canine alveolus.

S. rileyi is referred to the subgenus *Prosynthetoceras* because of its small size and lower crowned teeth as compared with *S. tricornatus,* and because of the retention of P^2 in the referred palate, MCZ 4065.

TABLE 3

Comparative measurements of *Synthetoceras* (*Prosynthetoceras*) *rileyi australis* in mm

	Synthetoceras (*P.*) *rileyi australis* MCZ 4065
Width of palate between M^1	64.5
P^3 to M^3 length	64.8
P^3 length	9.0
P^3 width	6.1
P^4 length	9.0
P^4 width	9.0
M^1 length	13.6
M^1 width	14.8
M^2 length	17.2
M^2 width	15.9
M^3 length	17.0
M^3 width	16.8

	Synthetoceras (*P.*) *rileyi australis*		*Synthetoceras* (*P.*) *rileyi rileyi*	
	MCZ 3654	MCZ 3708	MCZ 7635	AMNH 34181, type
Depth of jaw under P_2	21.2	22.7	22.5	19.3
Depth under P_4	23.6	—	23.0	20.5
Depth under M_3	29.1	27.5	28.4	—
P_2 to M_3 length	85.4	76.6	76.7	77.4
P_1 to P_2 diastema	42.0	46.0	46.1	—
P_2 length[a]	—	—	—	8.2
P_2 width[a]	—	—	—	3.1
P_3 length	—	8.5	—	9.7
P_3 width	—	4.0	—	4.3
P_4 length	10.5	10.5	10.1	10.4
P_4 width	6.5	6.3	5.7	6.4
M_1 length	13.0	12.2	14.4	12.4
M_1 width	10.0	9.2	9.4	9.4
M_2 length	18.0	16.1	15.4	16.7
M_2 width	11.0	10.5	21.6	22.4
M_3 length	25.5	25.0	21.6	22.4
M_3 width	11.4	11.1	10.5	10.1

[a] Known only from MCZ 3656; length, 8.2 mm, width, 4.0 mm.

MERYCOIDODONTIDAE
MERYCHYINAE
cf. MERYCHYUS sp.

An oreodont is represented in the Thomas Farm fauna by a single left upper molar, MCZ 7765, and an incomplete tarsus, MCZ 7766. In structure and size the molar (Fig. 3) most closely resembles *Merychyus minimus,* but is also quite similar to *M. elegans* of a later age. The external faces of the outer crescents are transversely concave and longitudinally convex, so that their apices overhang the internal crescents in typical oreodont fashion. The posterior crescents are narrower than the anterior pair and are relatively longer anteroposteriorly, as in M^3 of *M. elegans.* A strong cingulum is present on the anterior side of the protocone and a weaker one on the posterior side of the hypocone.

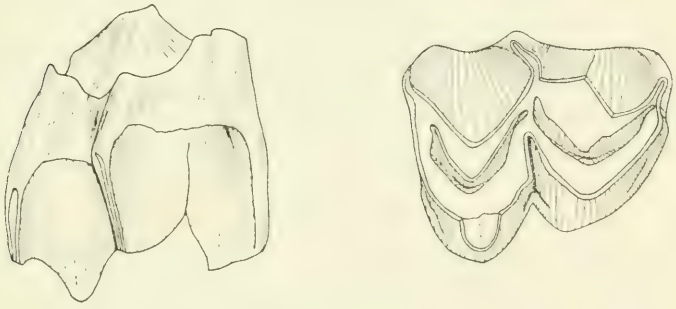

Figure 3. Oreodont upper left molar; cf. *Merychyus.* External view (left), and crown view (right), X1½.

There can be little doubt of the oreodont affinities of the tarsal elements, which probably belong to a single individual. The calcaneum is relatively short, strong, and laterally compressed with a strongly truncated proximal end which bears a deep groove for the tendon of the gastrocnemius. The sustentaculum is very small and only slightly projecting beyond the medial surface of the tuber. The astragalar facet on the sustentaculum is relatively long and narrow.

The astragalus is wide, low, and quite asymmetrical. The proximal trochlear is inclined at an angle to the distal one, and is placed more lateral in position as is typical of oreodonts. The sustentacular facet is narrow, occupying little more than half of the plantar surface.

These fragments are tentatively referred to the genus *Merychyus* because of the similarities to *M. minimus* in both size and morphology. However, a more certain reference must await more complete material.

The discovery of oreodont remains in Florida is a significant, although not a completely unexpected find. The apparent rarity of these animals in this region may not reflect their actual abundance. Schlaikjer (1935, p. 173) suggested that a gregarious habit combined with localized distribution and/or species habitat requirements of oreodonts could account for their great abundance in some areas, and relative rarity in others of the same age. As suggested by Thorpe (1937, p. 9) and Patterson (1949, p. 270), the absence of sediments deposited under appropriate conditions or their subsequent removal by erosion could be responsible for a meager oreodont fauna in certain areas. The idea, as proposed by Romer (1947, p. 10), that Florida was ecologically unfavorable for these animals is less attractive since the environment of the Florida Miocene was inferred partially by the absence of oreodonts. The rarity of this group from Florida beds is probably due to a combination of the first two factors: localized distribution and scarcity of sediments.

CERVIDAE

Blastomeryx (Parablastomeryx) floridanus White, 1940

Hypodigm: MCZ 3626, type, partial left mandible with P_4, M_1, the anterior external crescent of M_2, and the alevoli for P_2 and P_3; MCZ 3627, paratype, upper left molar; MCZ 3706, right mandible with dP_2 to M_3; MCZ 3707, left mandible with dP_3 to M_3; MCZ 3912, left mandible with dP_4 to M_3; MCZ 4220, left mandible with P_1, dP_3 to M_3; MCZ 4221, right mandible with P_3 to M_3; MCZ 4222, right mandible with P_2, M_1 to M_3; MCZ 7795, 23 astragali; MCZ 7796, 24 calcanea; MCZ 7797, 17 cubonaviculars; MCZ 7798, 103 proximal phalanges; MCZ 7799, 53 second phalanges; MCZ 7800, 24 ungual phalanges; MCZ 7801, 6 metapodials; MCZ 7802, left tibia; MCZ 7803, right radius.

Horizon and locality: Middle Miocene, Hawthorne Formation, Thomas Farm, Gilchrist County, Florida.

Diagnosis: White (1940, p. 34) diagnosed this species as follows: "A large *Parablastomeryx*, paraconid of P_4 with very small stylid, metaconid large and placed about the mid-length of the tooth, entoconid projecting at nearly right angles to the axis of the tooth, crest of hypoconulid extending along posterior border of the tooth nearly to the inner border."

Discussion: Since White's diagnosis, many new specimens have been collected. These demonstrate a remarkable degree of variation in the premolars and reveal the character of the lower molars and milk dentition, which were not available to him. The molars (Fig. 4) tend to confirm White's observation that *B. floridanus* is similar to *B. primus.*

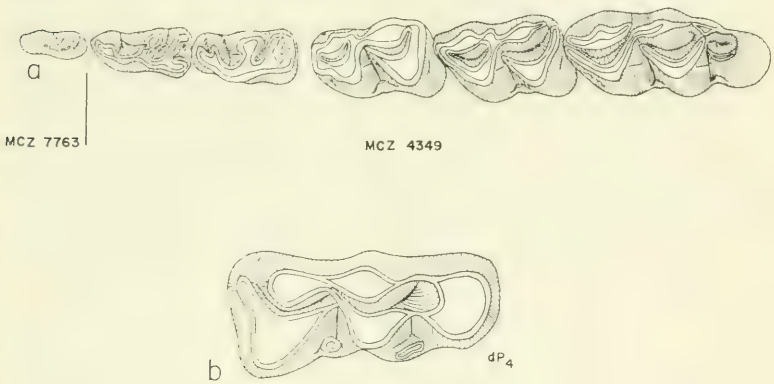

Figure 4. *Blastomeryx floridanus. a,* Composite crown view of left lower cheek teeth, X1½. *b,* MCZ 3706, right dP_4, X3.

The hypoconulid of M_3 has a prominent anterointernal cusp, and a strong palaeomeryx fold is present on the protoconid. The internal stylid of P_4 which White described as being "very small" on the type varies from strong on MCZ 7763 to absent on MCZ 4221. In P_3 of most of the specimens the entoconid is joined to the hypoconid by a semicircular crest around the posterior margin of the tooth, forming an enclosed lake. However, in MCZ 4349 the lake remains open posteriorly and is divided from the entoconid by a strong median ridge, which extends posteriorly to the end of the tooth and, after turning medially, ends in a minute capsule. These and other variants must be considered to be within the range of variation of this species since intermediate types link every extreme.

The lower milk teeth, dP_2 to dP_4 are known from two specimens, MCZ 3706 and 3707. DP_4 (Fig. 4b) is five cusped with an elongated pillar between the anterior inner cusps and a conical pillar between the posterior inner cusps. DP_3 is very similar to P_3 in structure and length, but is much narrower. There is little difference between dP_2 and P_2.

Because of the palaeomeryx folds, hypoconulid cusp, and relatively large premolars, this species is referred to the subgenus *Parablastomeryx*.

Referred postcranial material includes numerous tarsal bones, phalanges, a tibia, a radius, and several cannon bones. The tarsus is typically cervid. The tuber of the calcaneum is light and laterally compressed; the cuboid and navicular are solidly fused. The proximal phalanx is lightly built and considerably more slender dorsoventrally than in Recent cervids.

The metatarsals are fused along their entire length and there is a deep longitudinal groove on the dorsal side between metatarsal III and metatarsal IV. The distal facets are completely keeled, and together are considerably wider than the shaft. The metacarpals are fused and somewhat shorter than the metatarsals. The dorsal groove is shallow and indistinct. The tibia is long and slender, but less curved laterally than in Recent forms.

TABLE 4

Comparative measurements of *Blastomeryx* (*P.*) *floridanus* in mm

	MCZ 7763	MCZ 4221	MCZ 4349	MCZ 3626
Jaw and lower dentition:				
Jaw length	—	*132	—	—
P_2 to M_3	—	60.8	66.9	—
P_2 length	5.6	—	—	—
P_2 width	2.6	—	—	—
P_3 length	7.3	8.0	8.2	—
P_3 width	4.3	4.3	4.6	—
P_4 length	8.9	8.4	8.7	8.2
P_4 width	5.4	5.0	5.0	4.9
M_1 length	—	10.1	10.3	9.0
M_1 width	—	7.3	7.0	6.3
M_2 length	—	11.8	11.7	—
M_2 width	—	8.2	7.9	—
M_3 length	—	16.2	17.3	—
M_3 width	—	8.2	7.7	—

* estimated from incomplete specimen.

Machaeromeryx gilchristensis White, 1941

Hypodigm: MCZ 3651, type, partial right mandible with P_4 to M_2 and alveoli for P_2, P_3 and M_3; MCZ 3652, right mandibular fragment with M_1, and a left upper molar; MCZ 3709, partial right mandible with P_3 to M_2 and part of M_3; MCZ 3710, partial right palate with M^1 and M^2; MCZ 7804, 37 astragali; MCZ 7805, 1 calcaneum; MCZ 7806, 3 cubo-naviculars; MCZ 7807, 24 proximal phalanges; MCZ 7808, 5 second phalanges; MCZ 7809, 2 ungual phalanges; MCZ 7810, 1 metacarpal.

Horizon and locality: Middle Miocene, Hawthorne Formation, Thomas Farm, Gilchrist County, Florida.

Diagnosis: Premolar series relatively longer than in *M. tragulus,* M_2 shorter, upper molars less square with outer crescents considerably wider than inner ones, median pillars of upper molars only vaguely suggested in contrast to *M. tragulus.*

Discussion: No new information can be added to the diagnosis since this species remains so poorly represented. Aside from the differences in proportion, the teeth are very similar to *M. tragulus.*

The few tarsal remains and a referred metcarpal are essentially like those of *Blastomeryx,* but much smaller.

CONCLUSION

The fossil selenodont artiodactyls from Thomas Farm, Gilchrist County, Florida, indicate faunal communication with other parts of the North American continent during the Lower Miocene. *Synthetoceras r. australis* is at most subspecifically distinct from the western *S. r. rileyi,* and *Blastomeryx floridanus* and *Machaeromeryx gilchristensis* are close to western species. The specialized camelids, *Floridatragulus* and *Nothokemas,* are so far unknown in the West, but they or closely related forms have been recorded from the Oakville of the Texas coastal plain (Wilson, 1962). This contradicts White's contention that north-central Florida was an island until the end of Oak Grove time. Continuity, even if intermittent, between Florida and the mainland certainly seems to have occurred during the earlier Miocene. On geological grounds, Cook (1945) suggests that a narrow peninsula persisted through much of this period, and Bader (1956), on the basis of his comparisons of the Thomas Farm equids with those of Texas, states that isolation was, at best, very ephemeral. The opportunity for faunal movement between these areas, then, must have been considerably greater than suggested by White (1942).

REFERENCES

Bader, R. S.
1956. A quantitative study of the Equidae of the Thomas Farm Miocene. Bull. Mus. Comp. Zool., **115**: 49-78.

Cook, C. W.
1945. Geology of Florida. Bull. Florida Geol. Surv., No. **29**: 1-339.

Dougherty, J. F.
1940. Skull and skeletal remains of the camel *Paratylopus cameloides* from the John Day, Oregon. Carnegie Inst. Washington Publ. No. **514**: 49-58.

Fisk, H. N.
1940. Geology of Avoyelles and Rapides parishes. Bull. Louisiana Geol. Surv., **18**: 1-240.

Frick, C.
1937. Horned ruminants of North America. Bull. Amer. Mus. Nat. Hist., **69**: 1-669.

McKenna, M. C.
1966. Synopsis of Whitneyan and Arikareean camelid phylogeny. Amer. Mus. Novit. No. **2253**: 1-11.

Patterson, B.
1949. Rates of evolution in taeniodonts. Pp. 243-278. *In* G. L. Jepsen, G. G. Simpson, and E. Mayr eds., Genetics, Paleontology, and Evolution, Princeton Univ. Press.

Puri, H. S. and R. O. Vernon
1964. Summary of the geology of Florida and a guidebook to the classic exposures. Florida Geol. Surv., Special Publ. No. **5**: 1-312.

Ray, C. E.
1957. A list, bibliography, and index of the fossil vertebrates of Florida. Florida Geol. Surv., Special Publ. No. **3**: 1-175.

Renick, B. C.
1936. The Jackson group and the Catahoula and Oakville formations in a part of the Texas Gulf coastal plain. Univ. Texas Bull. No. **3619**: 1-104.

Romer, A. S.
1947. The fossil mammals of the Thomas Farm, Gilchrist County, Florida. Quart. Jour. Florida Acad. Sci., **10**: 1-10.

Schlaikjer, E. M.
1935. Contributions to the stratigraphy and paleontology of the Goshen Hole area, Wyoming, Part 4. Bull. Mus. Comp. Zool., **74**: 97-189.

Simpson, G. G.
1932. Miocene land mammals from Florida. Bull. Florida Geol. Surv., No. **10**: 11-14.

THORPE, M. R.
1937. The Merycoidodontidae, an extinct group of ruminant mammals. Mem. Peabody Mus. Nat. Hist., **3**: 1-428.

WHITE, T. E.
1940. New Miocene vertebrates from Florida. Proc. New England Zool. Club, **18**: 31-38.
1941. Additions to the Miocene fauna of Florida. Proc. New England Zool. Club, **18**: 91-98.
1942. The Lower Miocene mammal fauna of Florida. Bull. Mus. Comp. Zool., **92**: 1-49.
1947. Additions to the Miocene fauna of northern Florida. Bull. Mus. Comp. Zool., **99**: 497-515.

WILSON, J. A.
1962. Field trip no. 10, Tertiary formations between Austin and Houston, with special emphasis on the Miocene and Pliocene. *In* Geology of the Gulf Coast and Central Texas and a guidebook of excursions. Houston Geol. Soc., 1962: 342-354.

(Received 1 November, 1966.)

Errata

Page 6, Fig. 1*a*, for X4/5 read X2/5.

Page 10, Table 1, for P^1 length and width read P^2.

Page 11, Table 1. M_3 length, MCZ 4086, for 13 read 25; MCZ 4291, for 13 read 24.

Page 11, *Nothokemas*, line 8 (MCZ 4322) for P_2 to M_3 read P^2 to M^3.

Page 15, Table 2, M_1 width, AMNH 8197, for 14 read 9.5.

Page 17, lines 9, 10. MCZ 3655, for P_1 to M_3 and partial alveoli for I_2 to canine, read M_1-M_3 and alveoli for P_1-P_4.

Page 17, line 11, for MCZ 3666 read 3660.

Page 20, Table 3. M_2 width, MCZ 7635, for 21.6 read 10.3; AMNH 34181, for 22.4 read 10.4.

Page 22, *Blastomeryx*, Hypodigm. Add MCZ 7763, partial left jaw with P_2-P_4, and MCZ 4349, left jaw with P_3-M_3.

BREVIORA

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ANOLIS CHOCORUM, A NEW *PUNCTATUS*-LIKE ANOLE FROM DARIÉN, PANAMÁ (SAURIA, IGUANIDAE)

By Ernest E. Williams
and William E. Duellman[1]

INTRODUCTION

In the course of a survey of the herpetofauna of Panamá, the junior author, accompanied by Charles W. Myers, Tomás Quintero, and Linda Trueb, travelled in a dugout canoe from Santa María de El Real, Darién, to the upper part of the Río Tuira Basin in July, 1965. Most of the month of July was spent working out of a base camp at the confluence of the Río Tuira and the smaller tributary, the Río Mono. Collections also were made at the mouth of Quebrada La Plata lower on the Río Tuira, and on Cerro Quia on the Panamanian-Colombian border. Six specimens of a previously undescribed species of anole are included in the collection; these plus one specimen obtained by G. B. Fairchild at Tacarcuna, Darién, and three specimens obtained more recently from the Serranía de Pirre, form the basis for the present description. A long previously collected specimen from Colombia in the American Museum of Natural History (AMNH) proves to belong to the same species.

The junior author is grateful to his field companions, whose combined efforts made the trip a great success. The survey of the herpetofauna of Panamá is being conducted in cooperation with the Gorgas Memorial Laboratory in Panamá and is supported by a grant (NIH GM-12020) from the National Institutes of Health. This paper is one of a series of studies of the genus *Anolis* prepared by the senior author with the support of National Science Foundation Grant GB-2444.

The material of the new species has been divided between the Museum of Natural History, Kansas University (KU) and

[1] Museum of Natural History, University of Kansas, Lawrence, Kansas.

the Museum of Comparative Zoology (MCZ). We name the new anole for the Chocó Indians of the region:

ANOLIS CHOCORUM new species

Type. KU 96934, adult ♂, Río Tuira at Quebrada La Plata, 100 m, Darién, Panamá, collected by a native for Charles W. Myers, 26 July 1965.

Paratypes. Panamá: *Darién.* KU 76027, young ♂, Tacarcuna Village on Río Tacarcuna, 550 m, G. B. Fairchild coll., 9 July 1963; KU 96931, Río Tuira at Río Mono, 130 m, William E. Duellman coll., 12 July 1965; MCZ 82546, same locality, William E. Duellman coll., 13 July 1965; MCZ 82547, same locality, Charles W. Myers coll., 13 July 1965; KU 96932, Cerro Quia, 740 m, Charles W. Myers coll., 9 July 1965; KU 96933, same locality, Charles W. Myers coll., 26 July 1965; KU 98520, north end, Serranía de Pirre, 320 m, C. W. Myers coll., 15 January 1966; KU 98521, south ridge, Cerro Cituro, Serranía de Pirre, 1100 m, C. W. Myers coll., 23 January 1966; KU 98522, same locality, C. W. Myers coll., 25 January 1966. Colombia: *Chocó.* AMNH 18235, Atrato Drainage, Quesada River, R. D. O. Johnson coll., 6 November 1920.

Diagnosis. An *Anolis* related to *A. punctatus* Daudin and *A. transversalis* A. Duméril but differing from the first in coloration, and in having a large dewlap in the female, and the snout *not* swollen in the male; it differs from the second in lacking sexual dichromatism in dorsal pattern, and in a higher number of loreal rows, and in coloration. It differs from both species in a lower number of lamellae under phalanges 2 and 3 of fourth toe. See also Tables 1 and 2.

Description. (Paratype variation in parentheses.) *Head.* Head scales moderate to small, smooth. Fourteen (11-14) scales across snout between second canthals. Weak frontal ridges outlining a shallow frontal depression. Scales in frontal depression equal to or distinctly smaller than surrounding scales. Seven (7-9) scales border rostral posteriorly. Nasal scale separated from rostral by one to two scales. Six (5-7) scales between supranasals.

Supraorbital semicircles separated by three (1-3) scales, separated partly or wholly from the weakly differentiated supraocular disks by one (1-2) row of scales. One (1-3) elongate supraciliary continued posteriorly by granules. Canthus distinct, nine (8-10) canthal scales, the anteriormost very small. Loreal rows eight (7-9), the uppermost abruptly larger.

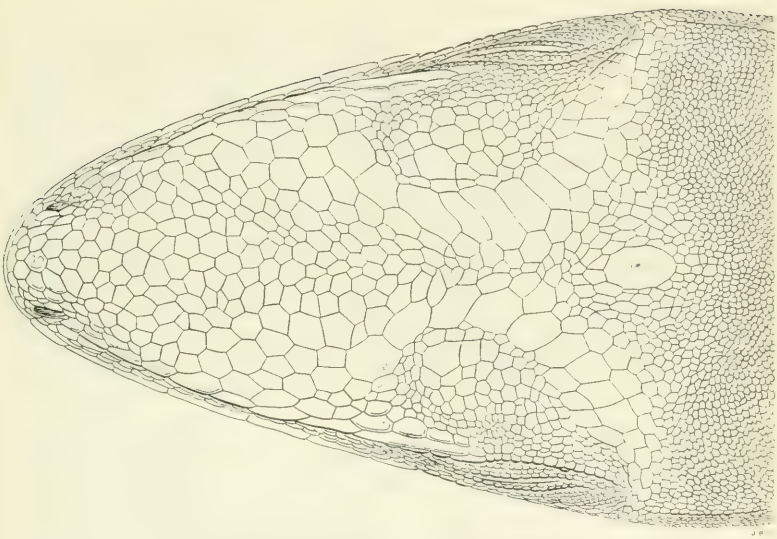

Fig. 1. *Anolis chocorum*, new species. Head scales of type, KU 96934. Actual snout-vent length 79 mm.

Temporal and supratemporal scales finely granular, several lines of weakly enlarged granules at the angle between temporal and supratemporal areas. Interparietal larger (or equal to, or smaller) than ear, separated from the supraorbital semicircles by four (2-4) somewhat enlarged scales. Laterally, slightly smaller scales grade into the supratemporal granules. Behind the interparietal the still smaller scales grade very quickly into granules as minute as those of the supratemporal area.

Three to four (2-4) suboculars in contact with the supralabials anteriorly, in contact with (or separated by 2-3 scales from) the canthus, posteriorly decreasing abruptly in size. Nine (8-9) supralabials to the center of the eye.

Limbs and digits: Hind foot scales multicarinate. Scales on anterior face of upper and lower arm, thigh and lower leg unicarinate, those at knee multicarinate. The larger scales of the hind limb as large or larger than the ventrals. About 20 (17-20) lamellae under phalanges 2 and 3 of fourth toe.

Tail: Tail slightly compressed. No dorsal crest, lateral and dorsal scales subequal. Two ventral rows larger, keeled. Verticils not evident. Postanal scales enlarged in male. Scales immediately behind vent smooth.

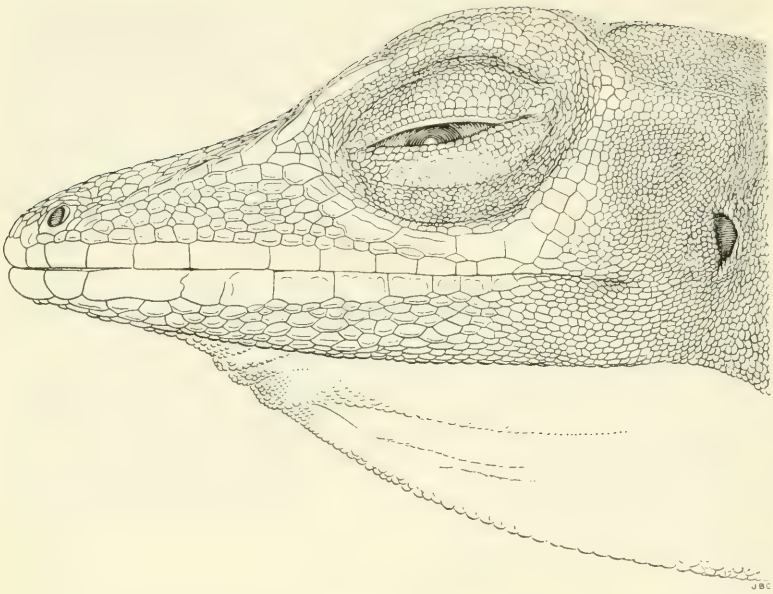

Fig. 2. *Anolis chocorum*, new species. Side view of head of type, KU 96934. Actual snout-vent length 79 mm.

Size (snout/vent length): ♂ (Type) 79 mm; longest ♀ 73 mm.

Color. Color in life is summarized in Table 3. The blue gray belly spotted with white is quite distinctive and differentiates this species immediately from any previously known.

As indicated in Table 3, the sexes differ most prominently in the color of the dewlap; it is in fact uncertain whether any other sex-correlated color differences exist. Both sexes vary somewhat in color; the occurrence in both of uniform and patterned dorsa is especially conspicuous. It is possible, however, that the pattern when present is feebler in females than in males; it is true in the specimens as preserved. Whether it was true in life is not recorded. Whether also some peculiar color variants (the light middle of the belly in some males and the gray tongue of one female) imply a range of variation in one sex not found in the other is unknown.

Ecology. The Darién localities from which *A. chocorum* is known are in a broad expanse of relatively undisturbed tropical

evergreen forest that is moderately well stratified and characterized by a lower story of slender palms in many places. The area has a definite, but not severe, dry season.

Anolis chocorum is arboreal. All individuals observed by day were in trees. One was obtained from the branches of a large tree immediately after it was felled. Another individual dropped from a tree during a storm at night. Two individuals were sleeping on bushes at night, one in a large fern on the steep bank of a mountain stream. Several species of *Anolis* are associated with *A. chocorum* in eastern Darién; these include two large arboreal species (*A. biporcatus* and *A. frenatus*), the moderate-sized arboreal *A. capito*, the smaller bush-dwelling *A. chloris, limifrons, tropidogaster*, and *vittigerus*, and the semi-aquatic *A. poecilopus*.

On July 10, 1965, Charles W. Myers found a striated egg partly concealed under loose bark on top of a rotting log on Cerro Quia. The egg was 16 mm x 12 mm; it hatched on July 26. The hatchling (KU 96933) had a snout-vent length of 30 mm and a total length of 92 mm. In coloration the hatchling resembled adults of *A. chocorum* by being green above with lateral diagonal rows of blackish brown spots. The tail was green with indistinct grayish brown crossbands. The venter was white with a faint bluish cast to the belly and a pale dull yellow cast to the median part of the dewlap.

Relationships. The series to which *A. chocorum* belongs is clearly an endemic South American one (see discussion of the alpha and beta series of Etheridge, 1960, in Williams, 1965). Its discovery in series in Darién is probably only an accident of activity and attention: similarly thorough and careful collecting has not been done in the adjacent areas of Colombia. However, a single specimen (AMNH 18235) records its presence there. This is a distribution resembling that of a number of other anoles. *A. chloris*, for example, associated in Darién with *A. chocorum*, is likewise a South American autochton, well known in Chocoan, Colombia (there known under the names *A. palmeri* and *A. gorgonae*), and in trans-Andean Ecuador. The distribution of *A. chocorum* may well be more like that of *A. chloris* than we now know and extend into western Ecuador. However, the range of *A. chocorum*, as at present known, is only eastern Darién Province in Panamá, where it occurs at elevations of from 100-1100 m, in the upper Río Tuira Basin and on the Pacific slopes of Cerro Quia and the Serranía del Darién, and in the Colombian Chocó.

Of the endemic South American group, *Anolis chocorum* is very clearly most similar to *Anolis punctatus* Daudin of Brazil, the

Guianas, Peru and Ecuador. The most immediately striking differences are in the coloration of the belly (blue gray with white spots) and in the lack of any snout swelling in the male. The presence of a much lower lamellar count and a large dewlap in the female are soon discovered as further differences.

A. punctatus is a species of the Amazonian-Guianan forests and the closest approach to the Darién-Chocó form thus far known is

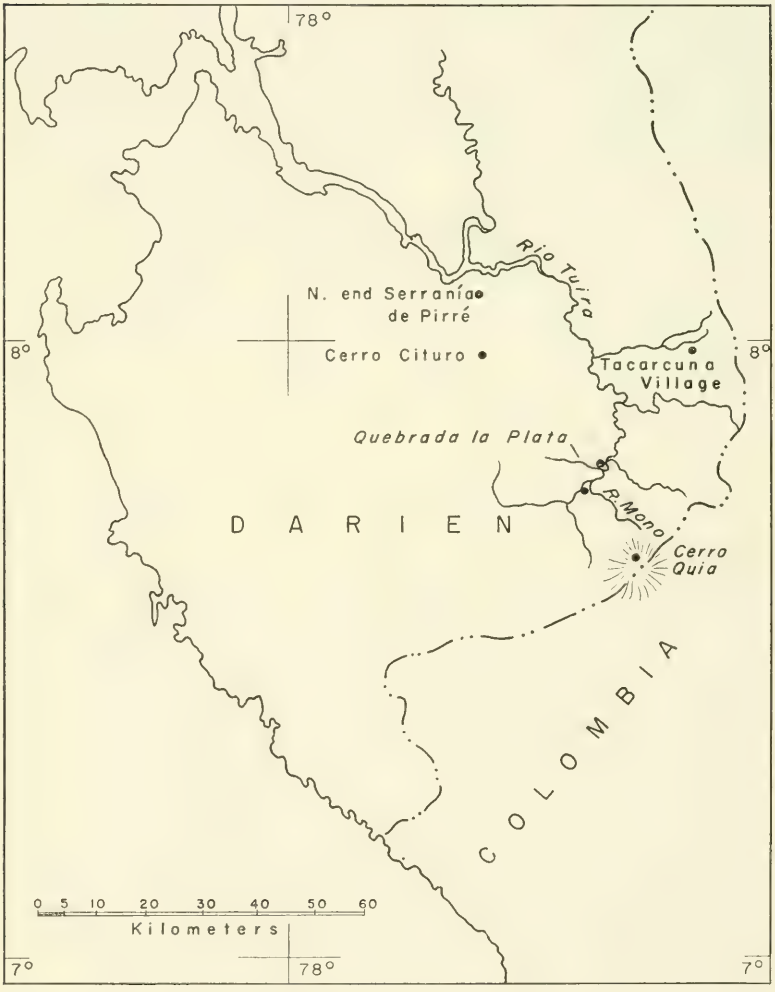

Fig. 3. Map of the distribution of *Anolis chocorum*, new species.

represented by a specimen from the Río Apaporis in eastern Colombia. Over most of its enormous range *A. punctatus* has smooth ventrals like *A. chocorum*. Some of the Peruvian, all the Ecuadorian, and the Colombian (Apaporis) populations have keeled ventrals. For these the subspecific name *boulengeri* is available.

Overlapping a substantial part of the western range of *A. punctatus*, all of *boulengeri*, and part of Peruvian typical *punctatus* is *A. transversalis*. Structurally, this differs from *A. chocorum* in lower loreal and toe lamellar counts and in the peculiar mental-postmental scale pattern. The very striking throat pattern of the female is very different from the condition of either sex in *A. chocorum* and the bold crossbanding of the dorsal surface of the female *transversalis* is also very different. The dorsal pattern of the male *transversalis* (originally described as a distinct species, *buckleyi*), however, does somewhat resemble the irregular spotted condition mentioned above as seen in some *A. chocorum*.

A. transversalis, so far as known, gets geographically no closer to *A. chocorum* than does *A. punctatus*. There is the very substantial gap in Andean Colombia.

The similarity in many scale characters of the three species is seen in Table 1 and is reinforced by the general similarity in habitus and size. *A. chocorum*, as shown in Tables 1 and 2, in many ways connects *A. punctatus* with *A. transversalis*.

The oblique rows of dark blotches on the dorsum of some specimens (well shown in the type, Fig. 1) resemble the dorsal pattern of the giant anoles, *A. frenatus, A. princeps, A. squamulatus, A. latifrons*. All of these have considerably higher scale counts in all respects than *A. chocorum*, and differ also in their much larger size (over 100 mm snout-vent length rather than 70-80 mm). They are, however, quite clearly closely related, and in mental shape, for example, are more like *A. chocorum* than are either *A. punctatus* or *A. transversalis*.

These apparent affinities of *A. chocorum* in several directions seem to effectively subvert the recent attempt of the senior author to define a *punctatus* group from which *A. transversalis* was expressly excluded as a "fringe species" and from which the giant anoles were considered still more remote. This newly discovered anole clearly and firmly connects the so-called "fringe species" (and the giant anoles as well) with the *punctatus* group. Thus we seem to be faced with a single series of species which, however, exhibit striking and peculiar trends in several adaptive lines. The presence of still surviving intermediates helps to connect up and to indicate the affinities of the more peculiar species.

TABLE 1

Scale Counts
Anolis chocorum and Relatives

	punctatus (including *boulengeri*)	*chocorum*	*transversalis*
Scales across snout between second canthals	8-14	10-14	4-8
Scales between semicircles	0-2	1-3	0-1
Scales between interparietal and semicircles	0-4	2-4	0-3
Loreals	4-7	6-8	3-6
Labials to center of eye	6-10	8-10	6-9
Lamellae, 4th toe	23-30	17-20	22-27

TABLE 2

Qualitative Characters
Anolis chocorum and Relatives

	punctatus (including *boulengeri*)	*chocorum*	*transversalis*
Snout	Swollen in ♂	Not swollen in either sex	Not swollen in either sex
Ventrals	Smooth (*punctatus*) or keeled (*boulengeri*)	Smooth	Smooth
Mental	At least as deep as wide	Wider than deep	Deeper than wide
Sublabials	+	—	+ (large)
Dewlap (♂)	Moderate (lateral scales large, elongate, in close-packed rows)	Large (lateral scales small, weak, in multiple rows widely separated by naked skin)	Large (lateral scales small, weak, in multiple rows widely separated by naked skin)
Dewlap (♀)	Absent	Large as in male but differently colored	Large as in male but differently colored
Dorsal pattern	Not sexually dichromatic	Not sexually dichromatic	Strong sexual dichromatism

TABLE 3

Color in life of *A. chocorum*

	♂	♀
DEWLAP		
	Edge anteriorly white, posteriorly orange	*Edge* white
	Sides pale orange with several faint bluish white or green lines	*Sides* green with white lines or pale green
	Base pale green	*Base* pale yellow or gray
DORSUM		
	Green, uniform or with oblique rows of dark green blotches on flanks	As in ♂
VENTER		
	Green of dorsum continued on edge of belly. Center of belly light or blue gray. Both blue and green areas heavily spotted with white	As in ♂, but center of belly not light in any specimen
EYELIDS		
	Edges yellow	As in ♂
IRIS		
	Pale brown (coppery) without dark markings	As in ♂, or reddish brown with gray periphery
TONGUE		
	Yellow orange, sometimes with tip dark gray	As in ♂, or pale flesh gray or pale greenish yellow or pale yellow
LINING OF THROAT		
	Black	As in ♂

REFERENCE CITED

WILLIAMS, ERNEST E.
1965. South American *Anolis* (Sauria, Iguanidae): Two new species of the *punctatus* group. Breviora, No. 233:1-15.

(Received 5 April, 1966.)

Fig. 4. *Anolis chocorum*, new species. Lateral view of type, KU 96934. Actual snout-vent length 79 mm.

Fig. 5. *Anolis chocorum*, new species. Ventral pattern of male type, KU 96934. Actual snout-vent length 79 mm.

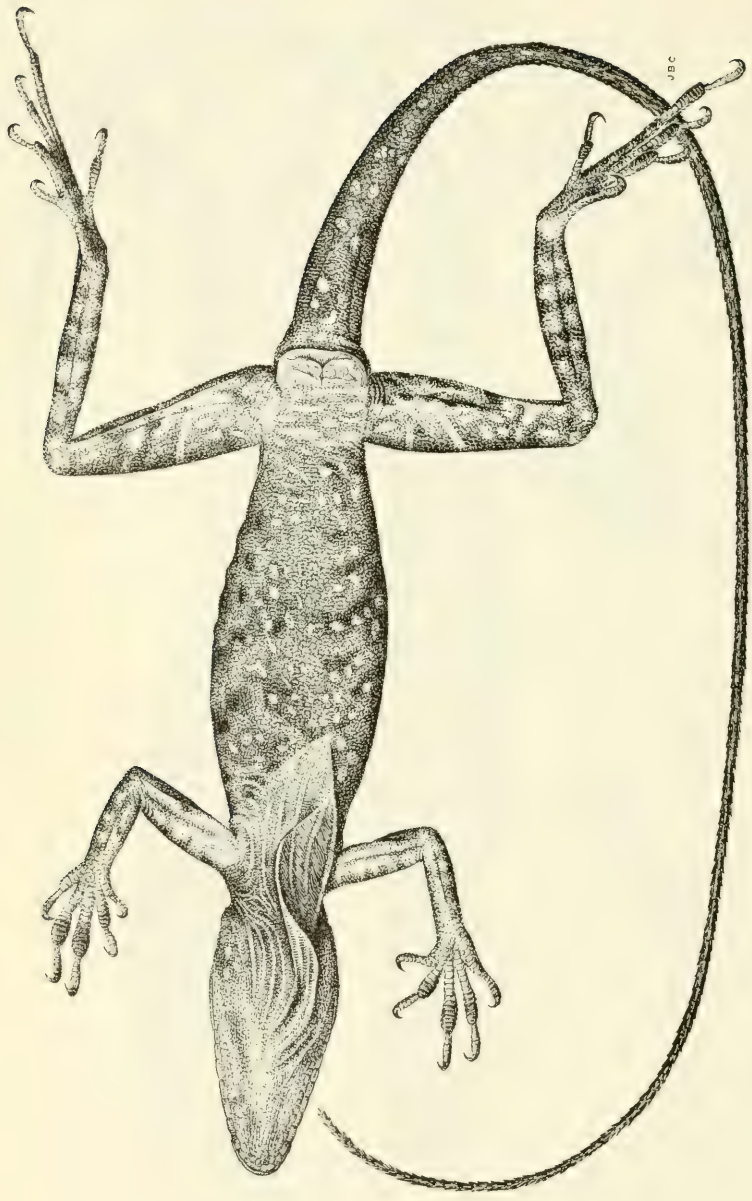

Fig. 6. *Anolis chocorum*, new species. Ventral pattern of female paratype, KU 96931. Actual snout-vent length 78 mm.

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Museum of Comparative Zoology

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A REVIEW OF THE CLARK FORK VERTEBRATE FAUNA

By Roger C. Wood

INTRODUCTION

The Clark Fork fauna, hitherto regarded as the standard for one of the provincial ages of the North American Continental Tertiary (Wood *et al.*, 1941, p. 9 and plate I), is known from only one area in the Bighorn Basin of northwestern Wyoming. In contrast to other Paleocene faunas representing provincial ages, no Clarkforkian quarry or pocket has yet been discovered. Consequently, this fauna has never been as well characterized as others in the standard sequence, and the validity of this provincial age has not been very well substantiated. This paper reviews previous work on the fauna and discusses some associated problems. Conclusions are based on field observations, a re-evaluation of the described collections, inspection of the original field notes, and unpublished annual reports of the Department of Vertebrate Paleontology of the American Museum of Natural History.

Professor Glenn L. Jepsen suggested this problem as a senior thesis topic while I was an undergraduate at Princeton. His generosity in permitting me access to Princeton's valuable collection of Paleocene fossils is here gratefully recognized. Dr. Malcolm C. McKenna of the American Museum of Natural History most kindly made available for study the specimens upon which the original Clarkforkian faunal description was based; I have also profited from discussions with him. I am much obliged to Professors Bryan Patterson, George Gaylord Simpson, Albert Wood, and Dr. Leigh Van Valen for criticisms and suggestions concerning this manuscript. In addition I am grateful to Dr. Giles MacIntyre, who found the map used by Walter Granger in the Bighorn Basin during the field seasons of 1910 through 1912. A portion of this map is reproduced in Figure 2. The hospitality of the Churchill family of Powell, Wyoming, added considerably to the enjoyment of

doing field work during the summers of 1961 and 1962. I would also like to thank Mrs. Frances Wood and Miss Margo Hayes for typing the numerous revisions of this paper.

Financial assistance provided from the John Boyd Fund of Princeton University enabled me to spend the latter part of the summer of 1961 and the entire field season of 1962 in the Bighorn Basin, working in the type areas of the Clark Fork fauna. Support from the National Science Foundation training grant for evolutionary biology at Harvard University was helpful during the final stages of my research.

Abbreviations used in this paper are as follows: AMNH, American Museum of Natural History; PU, Princeton University; FMNH, Field Museum of Natural History; USNM, United States National Museum.

HISTORY OF STUDY

During the summers of 1910 through 1913, and again in 1916, field parties sponsored by the American Museum of Natural History conducted extensive investigations of the Tertiary sediments of the Bighorn Basin. Some of the results were published by Sinclair and Granger in 1912; of interest to the present study was the recognition of a new vertebrate fauna occurring near the top of the Fort Union.[1] Specimens comprising the fauna were obtained from three different localities whose approximate positions, determined from the following descriptions, are labelled A, B, and C on the accompanying map (Fig. 1). These areas were described (Sinclair and Granger, 1912, pp. 59-60) as being ". . . on the southwest slopes of McCulloch Peak . . . about a mile due east of the point where the Fort Union-Wasatch contact line crosses the Shoshone River, 245 feet stratigraphically below the contact with the red-banded beds [A]; on the north side of the Shoshone River in the bluffs opposite Ralston station [B]; to the northwest of Ralston on Big and Little Sand Coulee [C]." Only the McCulloch Peak locality (A) was regarded as being unquestionably Paleocene; some uncertainty was expressed concerning the exact stratigraphic position of the other two areas. This doubt led the authors to conclude ". . . we feel that further examination of the stratigraphy is desirable. Should the beds in question prove to be older than the Knight [early Eocene], and it be deemed advisable to give them a formation name, they may be referred to as the Ralston beds or Ralston formation."

[1] The Paleocene rocks in this area have been referred to as the Polecat Bench Formation; see Jepsen, 1940.

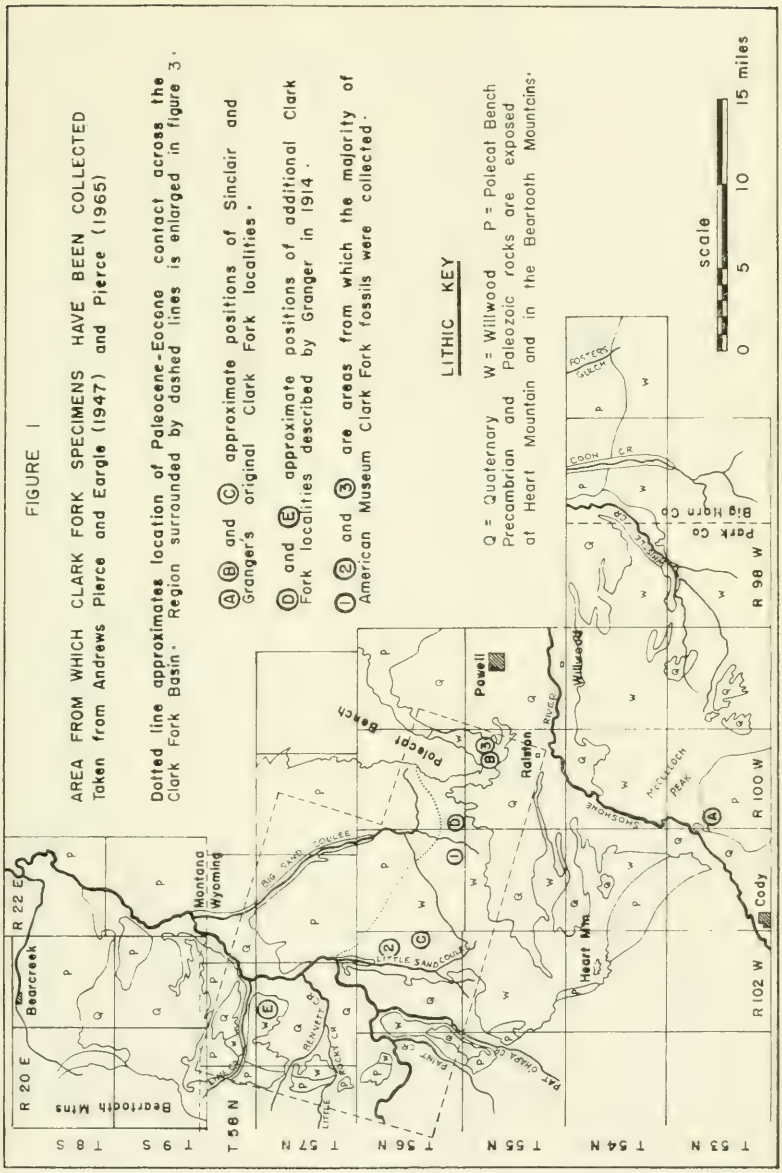
FIGURE 1
AREA FROM WHICH CLARK FORK SPECIMENS HAVE BEEN COLLECTED
Taken from Andrews Pierce and Eargle (1947) and Pierce (1965)
Dotted line approximates location of Paleocene-Eocene contact across the Clark Fork Basin. Region surrounded by dashed lines is enlarged in figure 3.
(A) (B) and (C) approximate positions of Sinclair and Granger's original Clark Fork localities.
(D) and (E) approximate positions of additional Clark Fork localities described by Granger in 1914.
(1) (2) and (3) are areas from which the majority of American Museum Clark Fork fossils were collected.
LITHIC KEY
Q = Quaternary W = Willwood P = Polecat Bench
Precambrian and Paleozoic rocks are exposed
at Heart Mountain and in the Beartooth Mountains.
scale
0 5 10 15 miles
R 20 E
R 22 E
R 102 W
R 100 W
R 98 W
T 58 N
T 57 N
T 56 N
T 55 N
T 54 N
T 53 N
T 8 S
T 9 S
Bearcreek
Beartooth Mtns
Montana
Wyoming
Cody
Powell
Ralston
Willwood
Heart Mtn.
Polecat Bench
Big Horn Co
Park Co
BIG SAND COULEE
LITTLE SAND COULEE
PAINT CR
PAT CHAVA CR
SHOSHONE RIVER
McCULLOCH PEAK
SOOH CR
ROGERS GULCH

A more precise definition of this fauna was subsequently published by Granger in 1914. Further collecting had increased the number of specimens to fragments "representing nearly 200 individuals" (Granger, 1914, p. 204). Characterized by the absence of perissodactyls, artiodactyls, rodents and primates (the last two not then known from Paleocene deposits), the fauna was composed predominantly of representatives of two genera, *Phenacodus* and *Ectocion,* which constituted over three-fourths of the collection. The rest of the fauna included some Paleocene genera, whose range was known to extend into the overlying Eocene Gray Bull beds, and genera of Gray Bull age. Assignment of the fauna to an appropriate epoch was supposedly aided by the abundant presence of the reptilian genus *Champsosaurus,* which was at the time considered to be a distinctly Cretaceous and Paleocene genus. This evidence, coupled with the absence of the four orders of mammals previously mentioned, inclined Granger to regard these beds as being of late Paleocene rather than early Eocene age.

Because the name "Ralston" was preoccupied by a group of Pennsylvanian rocks, Granger substituted in its place the term "Clark Fork" beds. These sparsely fossiliferous strata were estimated to attain a maximum thickness of 500 feet. Besides the McCulloch Peak locality (A), exposures were prominent "In the bluff [Polecat Bench] in the northern part of the Bighorn Basin" where "characteristic fossils were found as far east as a point north of Powell [i.e. in beds extending northeast from B]." In addition, two new localities were described: "In the Clark Fork basin the fossils were obtained from both sides of the wagon road where it drops down to the Big Sand Coulee from the Bighorn Basin divide, also from . . . the opposite side of Clark Fork River between the mouths of Line and Little Rocky Creeks" (*Ibid.,* p. 204). These last areas, not mentioned in Sinclair and Granger's paper, are marked on the map as localities D and E.

Descriptions of the various new types ascribed to the Clark Fork fauna appeared in a series of papers by Matthew (1915a, b, c; 1918) and Granger (1915), and in one by Simpson (1929). It is interesting to note Simpson's remark (p. 2) that some of the specimens being described might be from the lowest Eocene Sand Coulee horizon rather than from the Clark Fork. However, no reason was given for this statement.

Not until 1930 was a complete faunal list published (Jepsen, 1930b, pp. 492-493), which included several species collected by Princeton University field parties subsequent to the American Museum's initial discoveries. Three new forms were described,

the most significant for this study being *Dipsalodon matthewi,* the only genus restricted to the Clark Fork. In addition, note was made of the fact that *Champsosaurus* could no longer be used to demarcate the upper limit of Paleocene beds, thus invalidating Granger's premise that this genus could be used for distinguishing between Paleocene and Eocene sediments.

Revision of the Clark Fork fauna was undertaken by Simpson (1937). Several forms from the original collection were for the first time described. In addition, one species, *Ambloctonus priscus* Matthew (= *Palaeonictis occidentalis* Osborn; Denison, 1938, p. 175), was removed from the fauna on the grounds that field records associated with the specimen clearly indicated that it belonged with the Sand Coulee fauna. A further deletion from the fauna was made by Jepsen, who removed *Parectypodus,* the only multituberculate that had been regarded as part of the fauna, because its original inclusion had resulted from "an error in locality identification" (Jepsen, 1940, p. 324). No additions or deletions to the fauna have subsequently been published.

INTERPRETATION OF MAPS

Since Granger used only verbal descriptions, rather than section, township, and range data for indicating the locations of specimens and type areas, great value must be attached to the recent finding of his original field map, part of which is reproduced as Figure 2. Its discovery permits much greater confidence in the determination of some of the areas where the original Clark Fork collections were made. No date appears on the map, which was taken from Fisher's 1906 report. Perusal of the field notes, however, indicates that Granger was in this part of the Bighorn Basin only in 1911 and 1912. Therefore, it seems reasonable to infer that the hachures sketched on his map, undoubtedly intended to indicate badlands, correspond to areas prospected in those years. These badlands, consequently, must represent the type localities for the Clark Fork and Sand Coulee beds described by Sinclair and Granger (1912) and Granger (1914). Some of these hachures coincide with the placement of letters B, C, D, and E on Figure 1, thus confirming the positions of most of Granger's type localities. Unfortunately, uncertainty must still remain as to the exact location of the area on the southwest slopes of McCulloch Peak (indicated approximately in Figure 1 by the letter A) because no hachures were drawn on this part of Granger's map.

Confusion may be averted by noting the following problems concerning the same name for different places on various maps.

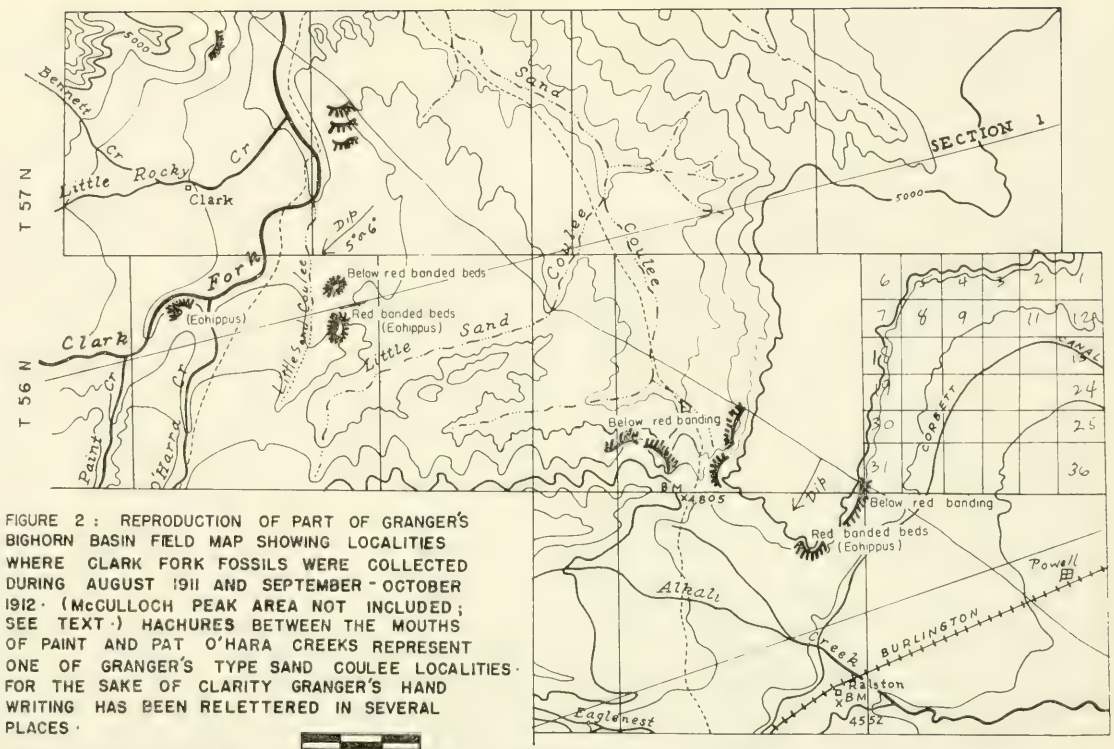

FIGURE 2: REPRODUCTION OF PART OF GRANGER'S BIGHORN BASIN FIELD MAP SHOWING LOCALITIES WHERE CLARK FORK FOSSILS WERE COLLECTED DURING AUGUST 1911 AND SEPTEMBER - OCTOBER 1912. (McCULLOCH PEAK AREA NOT INCLUDED; SEE TEXT.) HACHURES BETWEEN THE MOUTHS OF PAINT AND PAT O'HARA CREEKS REPRESENT ONE OF GRANGER'S TYPE SAND COULEE LOCALITIES. FOR THE SAKE OF CLARITY GRANGER'S HAND WRITING HAS BEEN RELETTERED IN SEVERAL PLACES.

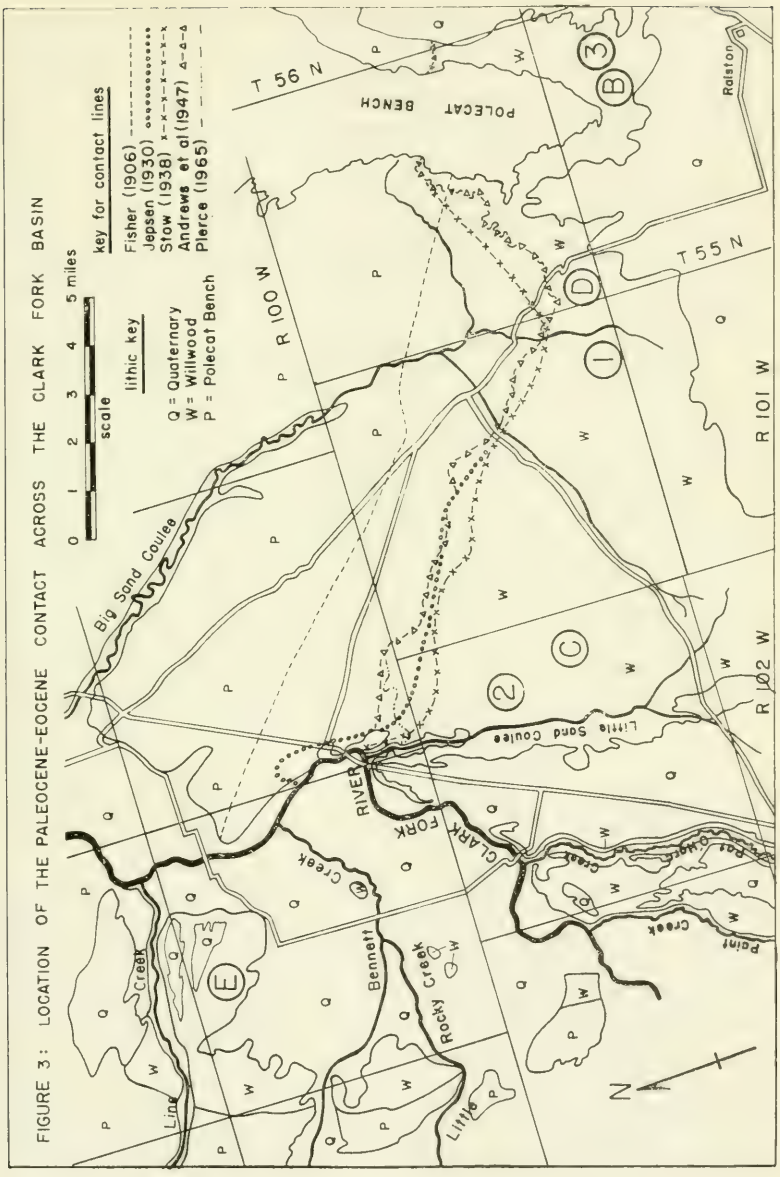

FIGURE 3: LOCATION OF THE PALEOCENE-EOCENE CONTACT ACROSS THE CLARK FORK BASIN

On Fisher's map (1906; see Fig. 2), Bennett Creek is shown as a tributary of Little Rocky Creek. All subsequent maps, however, depict Little Rocky Creek as being a tributary of Bennett Creek (see Fig. 1). Furthermore, Fisher's map indicates Little Sand Coulee as being a branch of Big Sand Coulee, but in the Annual Report of the Department of Vertebrate Paleontology for 1912, Granger remarks that ". . . What is known locally as Little Sand Coulee [is] not the Little Sand Coulee of Fisher's map." The actual location of the coulee is written on Granger's field map (see Fig. 2), and later maps all follow Granger's positioning of the coulee.

A final problem is the question of where the Paleocene-Eocene contact in the Clark Fork Basin is situated. The first geological map of the area was published by Fisher in 1906. Presumably the contact there drawn (refer to Figure 3 for position of this and subsequent contact lines) represented only a rough estimate, as the line across the basin is unnaturally straight, and no discussion of the means by which the contact was detected are included in Fisher's report. Sinclair and Granger (1912) apparently did not take Fisher's contact very seriously, since, with the exception of the McCulloch Peak locality, the beds they describe as having yielded their presumably Paleocene Clarkforkian material are located several miles to the southwest of Fisher's line, well into his Eocene, as can be seen by referring to Granger's field map (Fig. 2). Their 1912 paper, however, includes a sketch map which shows a contact coinciding with that of Fisher's map. In 1930 Jepsen published a map whose Paleocene-Eocene contact lay several miles southwest of and parallel to that recognized by Fisher. The line was drawn more precisely on the basis of paleontological evidence, using the conventional criterion that the lowest Eocene beds are marked by the first appearance of *Hyracotherium*. Agreeing relatively closely with Jepsen's contact is one drawn by Stow (1938) on the basis of the presence or absence of certain types of heavy minerals that he thought permitted differentiation between Paleocene and Eocene sediments. Although apparently unaware of Jepsen's and Stow's works (as their papers are not indicated as being sources of data), Andrews, Pierce, and Eargle (1947) drew a contact closely paralleling these previous ones, but generally slightly to the northeast. For that part of the basin shown on the map, Pierce (1965) indicates minor deviations from his previously drawn contact except in the area directly east of the mouth of Little Sand Coulee, where his boundary diverges appreciably from the earlier one. Thus, the boundary between

Paleocene and Eocene beds has been reasonably clearly established within rather narrow limits. The area where the greatest divergence exists between the various lines, however, is to the east of the mouth of Little Sand Coulee, a fact which is of some importance concerning the provenance of about half the specimens in the Princeton collection (see p. 21).

THE AMERICAN MUSEUM COLLECTION

Data concerning the American Museum's Clark Fork collection are summarized in Table I. One fact readily apparent from this table is that there are only 89 specimens in the original collection, not the "nearly 200" mentioned by Granger. This observation may indicate that many specimens, in addition to the one discussed by Simpson (1937; see above, p. 5), have been at one time or another removed from the fauna without this action having been noted in any publication. On the other hand, it may merely indicate that Granger had overestimated the size of the collection. At any rate, the basis available for defining and characterizing the type collection is less than half as large as published data indicate.

An additional feature worthy of note is the nature of the specimens from the McCulloch Peak area (A, Fig. 1); these are described in Table I, footnote 10. The identifiable fragments include no elements restricted to the Paleocene. This fact lends itself to some interesting speculation, as this locality is the only one of the three originally described by Sinclair and Granger as representing unquestionable Paleocene sediments. In this connection some of Granger's comments in the 1911 Annual Report of the Department of Vertebrate Paleontology are most informative: "These beds [at Ralston] proved to be of the same age as those [from the base of McCulloch Peak] described above and although fossils were scarce some 50 individuals were obtained. The small phenacodonts constituted about ½ the entire number and there still was no trace of Perissodactyla, of Artiodactyla, nor Rodentia. The presence of *Bathyopsis, Limnocyon*, and a *Metacheiromid* were surprising, considering that the beds lie below the Wasatch. . . . The dip of the [Ralston] beds where exposed would carry them below the Wasatch at the base of McCulloch Peak, allowing no fault or change in dip." In other words, Granger apparently considered that the fauna contained in the beds north of Ralston included various forms that he would have expected to find in typical early Eocene sediments. Thus the Clark Fork beds were defined on the basis of negative evidence, i.e., what had not been

TABLE I

THE AMERICAN MUSEUM CLARK FORK COLLECTION

Information taken from field labels associated with the specimens, and also from Denison (1938) and Simpson (1937 and 1943).

SPECIES (Numerals opposite each name indicate the number of specimens from each locality.)	LOCALITIES				
	head of Big Sand Coulee (Locality #1 on map)	east, or three miles east, of mouth of Pat O'Hara Creek (Locality #2 on map)	bluff NE of Ralston; N, or three miles N, of Ralston (Locality #3 on map)	Clark Fork beds, "period," or formation	other
Apheliscus nitidus	1				
Coryphodon sp.	1				1
Didymictis protenus proteus[1]	6		2	6	
Dipsalodon matthewi[2]			1		
Dissacus praenuntius[3]				2	
Ectocion osbornianus ralstonensis	14	4	2		1
Esthonyx[4]					
grangeri	4	1			
latidens	1	1			
cf. *spatularius*			1	1	
not specifically identified	1		1		

Haplomylus speirianus	2		1		
Meniscotherium priscum[7]	1				
Oxyaena aequidens	2			1	1
Oxyaena platypus[6]			1	1	
Palaeanodon parvulus	1				
Palaeoryctes punctatus[7]	1				
Phenacodus primaevus cf. *primaevus*[5] *primaevus* cf. *intermedius*	5	4	4	1	1
Plesiadapis cookei				1	
Plesiadapis dubius			1		
Probathyopsis praecursor[9]	4		1		1
Thryptacodon antiquus		2			
TOTAL[10]	44	12	15	13	5

[1] Fourteen specimens in the Clark Fork collection are labelled as belonging to this subspecies, although Simpson (1937, p. 16) mentions the existence of only five. Six specimens, including the type, are from "Clark Fork beds, head of Big Sand Coulee," a locality within the Gray Bull beds (see p. 14). It is not possible to determine in which beds the other eight specimens were found (pp. 17, 18). Simpson observed (1937, p. 15) that "The Clark Fork specimens are within the range of those from the Gray Bull in every dimension." However, he cites evidence, from measurements of M_2, which he felt required the establishment of a distinct subspecies. Since at least some of the "Clark Fork" specimens are from Gray Bull beds, this distinction between the "Clark Fork" and Gray Bull subspecies would seem to be invalidated, all specimens being referable to the Gray Bull form *D. protenus*.

Footnotes for Table I (continued)

[2]Denison (1938, p. 175) states: "Amer. Mus. No. 16068 from the Clark Fork horizon, described by Matthew . . . as '?*Oxyaena* sp. innom.', is referred here doubtfully to *Dipsalodon*. It includes much worn upper teeth of approximately the same size as *D. matthewi*." Van Valen (1966, p. 82) has referred this specimen to *D. matthewi*.

[3]AMNH No. 18668 has been tentatively referred to this genus, but specific identification is difficult because of the scrappy nature of the specimen.

[4]Simpson (1937) recognizes three, or possibly four, species of *Esthonyx* from the Clark Fork beds: *E. bisulcatus, E. grangeri, E. latidens,* and perhaps *E. spatularius*. AMNH No. 16065 is labelled as "*E.* cf. *spatularius* (type)," but is figured in Simpson (1937, p. 6, fig. 1) as *E. ?bisulcatus*. However, this specimen could not be the type for either species since it was found in 1912, while the two species in question were described by Cope in 1874 and 1880, the type for *E. spatularius* being AMNH No. 4809 and that for *E. bisulcatus* being USNM No. 1103 (Gazin, 1953, pp. 17, 21). None of the specimens in the collection are presently labelled as representing *E. bisulcatus*.

[5]Jepsen (1930b, p. 493) listed this species as being included in the American Museum's collection although Simpson (1937) does not include it in his Clark Fork faunal list. However no mention or reason for its deletion is given. Gazin (1962, p. 67) notes that "the type of *M. priscum* from the Clark Fork beds could not be located in the American Museum collections." Personal investigation has confirmed this report.

[6]Denison (1938, p. 167) referred Matthew's type of *Dipsaladictis platypus* (AMNH No. 15857) to this species, stating that "it is definitely an oxyaenine, which differs from other primitive species of *Oxyaena* only in its smaller size." One additional specimen (AMNH No. 18667) is labelled as belonging to this species.

[7]This specimen (AMNH No. 15850) was listed as "Nyctitheriidae genus and sp. indet." by Simpson (1937, p. 4), but has been described as *Palaeoryctes punctatus* by Van Valen (1966, p. 56).

[8]Many *Phenacodus* specimens are represented as disarticulated bones or miscellaneous tooth and jaw fragments rather than as associated sets of teeth or bones. Individual fossils were labelled variously as *Phenacodus, P. primaevus, P. intermedius,* and *P. hemiconus,* and thus do not concur with the two subspecies included in Simpson's 1937 faunal list.

[9]Only two specimens in the collection are labelled as *Probathyopsis praecursor*. Four other specimens in the collection are labelled *Bathyopsis* or Bathyopsidae. The latter fossils were clearly intended by Simpson to be included in the new genus since one of them comes from opposite the mouth of Little Rocky Creek, one of the localities mentioned as an area where specimens of this species had been found, and it is in fact the only specimen of any kind from this area. For another of the four localities listed

as having yielded *P. praecursor* remains, three miles east of the mouth of Pat O'Hara Creek (locality 2, Fig. 3), no Clark Fork specimens could be located. Simpson suggested (1929, p. 2) that "Some of this material may be from the Sand Coulee horizon." Four specimens, including the type, are from locality 1 (Fig. 3), confirming the idea that at least some of the specimens are part of an early Eocene fauna rather than a late Paleocene Clark Fork one.

[10] In addition to the specimens listed in the chart, the following material is included in the collection: three boxes of "miscellaneous bones and teeth" from the west slope of McCulloch Peak, containing fragments identifiable only as *Champsosaurus, Phenacodus, Ectocion,* and a pantodont; four boxes of miscellaneous fragments labelled only as being from the "Clark Fork Basin," and another from "north of Ralston." None of this fragmentary material would appear to affect the conclusions based on analysis of the better specimens in the collection, and hence has not been discussed.

found in them, rather than on fossils actually contained in them which could be characterized as having a distinctive Paleocene aspect. Since the type fauna was principally found in strata whose position in the section was by no means certain, and since the fauna from the only site regarded by Granger as being definitely of Paleocene age had no obvious Paleocene affinities, it is not at all certain whether or not a Clark Fork fauna can in fact be distinguished.

Examination of the labels accompanying the specimens in the American Museum's Clark Fork collection reveals that over 85 per cent of the fossils, acquired in the years 1910-1916, were found at three sites. These localities were:

(1) the head of Big Sand Coulee (Area D, Fig. 1);

(2) east, or three miles east, of the mouth of Pat O'Hara Creek (Area C, Fig. 1);

(3) north, or three miles north of Ralston; or bluff, or base of bluff, northeast of Ralston (Area B, Fig. 1).

For convenience of reference, American Museum specimens from these areas will henceforth be designated merely as being from locality number 1, 2, or 3 (see Fig. 1).

Locality number 1 is in the region characterized by Granger as the type area of the lowest Eocene Sand Coulee beds (1914, p. 205). "Near the head of Big Sand Coulee in the Clark Fork basin there is a series of about 200 feet of red-banded shales lying

between the gray shales[1] of the Clark Fork and the *Systemodon*-bearing gray shales above which are referred to the Gray Bull beds. The outcrop of these red-banded beds extended, from the high bluff on the south side of the Coulee, in a northwesterly direction across the basin for several miles." Furthermore, in this same paper, Granger describes (p. 203) the Gray Bull beds and mentions various areas where they outcrop. "In the Clark Fork basin they are exposed in the southwestern part along the heads of Big and Little Sand Coulees, where they are of a uniform gray color instead of the usual gray, red, and yellowish banding." Reference to all the geologic maps of this part of the basin shows that the Paleocene-Eocene contact line crosses the southern branch of Big Sand Coulee approximately two miles below its head, and the western branch nearly five miles from its head. The eastern prong of the coulee, of which the one on the map is only one of many, is probably not that referred to on the labels, since its head originates at the base of Polecat Bench and such a fact would have made a convenient reference for the labels. As Granger noted the misidentification of Little Sand Coulee on his field map (refer to p. 8 and Fig. 2), he may have been talking about either the southern or western branches of Big Sand Coulee. However, whichever of these two is chosen, the locality would be well into Eocene Gray Bull or Sand Coulee strata. In view of the fact that Granger's field map indicates an extensive area of prospected exposures at the head of the southern branch of Big Sand Coulee, and none are marked near the head of its western fork, it is most probable that this area is the one in question. There is no doubt at present that these are Gray Bull beds.

In addition, many specimens in the American Museum collections labelled as "Wasatch," "Sand Coulee," or "Gray Bull" are noted also as having come from "the head of Big Sand Coulee." For example, the label accompanying the type of *Apheliscus nitidus* (AMNH No. 15849, listed in Table I) reads "Clark Fork formation, Clark Fork, Wyoming, 1911, head of Big Sand Coulee." That accompanying another specimen of the species, AMNH No. 16925, reads "Wasatch formation, Sand Coulee Beds, Clark Fork,

[1] Jepsen has pointed out that it is impossible to use color banding for distinguishing Clark Fork from overlying beds, since ". . . red strata occur well down in the Clark Fork beds" (1940, p. 237; see also 1930b, p. 493).

Wyoming, 1913, head of Big Sand Coulee." All other specimens of *A. nitidus* are similarly labelled as being from Gray Bull beds. It would therefore appear that the two cited specimens, although labelled as being from two different horizons, are most probably from the same one, the Gray Bull. Consequently, based on the evidence revealed by the specimen labels, it is probable that all supposed Clark Fork fossils labelled as having been found at the "head of Big Sand Coulee" should more properly be referred to the lower Gray Bull or Sand Coulee beds. Since half of Sinclair and Granger's original Clark Fork fauna (see Table I) was obtained from the vicinity of the head of the Coulee, it is likely that these specimens are part of one or more early Eocene faunas rather than of a late Paleocene Clark Fork fauna.

"East [or three miles east] of the mouth of Pat O'Hara Creek" (locality 2) is an area lying in an extensive series of Willwood exposures. This locality, as is true for locality 1 also, was never mentioned by Granger as one of the five type areas (A through E, Fig. 1) for the Clark Fork beds. Granger's field map (Fig. 2) shows two sets of badlands sketched along a north-south axis in this region, the southern one being labelled "red-banded beds" and the northern one "below red-banded beds." These may be interpreted in the light of Granger's remarks in the 1913 Annual Report of the Department of Vertebrate Paleontology: "Section across Clark Fork Basin from head of Little Sand Coulee northeast to mouth of Big Sand Coulee:

Wasatch — gray shales — 500+ feet
[Sand Coulee] — red-banded shales — 200 feet
Ralston — gray shales — 500+ feet."

Clearly, the red-banded beds must represent some of Granger's Sand Coulee exposures. Consequently, the beds farther north can only be regarded as Clark Fork beds, and it seems reasonable to assume that locality 2 corresponds to this area, which has always been mapped as being covered by Eocene beds (Fig. 3). It seems curious that part of a fauna purported to be of latest Paleocene age should be derived from sediments whose presumed early Eocene age has never been questioned. With respect to this paradox, an examination of the specimens from locality 2 is most instructive. Reference to Table II reveals that all of the Clark Fork fossils from locality 2 are also known from the Sand Coulee or Gray Bull, and often from both of these horizons. In fact, the one specimen of *Phenacodus hemiconus* from this locality was apparently regarded by Granger as being of Gray Bull provenance,

TABLE II

SPECIMENS IN THE AMERICAN MUSEUM CLARK FORK COLLECTION FROM LOCALITY 2

SPECIES (Identifications are taken from the labels associated with the fossils)	REFERRED SPECIMENS (AMNH)	HORIZONS IN THE CLARK FORK BASIN FROM WHICH THE SPECIES IS KNOWN
Ectocion ?osbornianus	16047	Clark Fork, Sand Coulee, Gray Bull (Granger, 1915, p. 352)
Ectocion ralstonensis	16046, 16061	Clark Fork, Sand Coulee, Gray Bull (Granger, 1915, p. 353)
Ectocion	1 unnumbered	Not specifically identified; thus nothing can be said about its range.
Esthonyx grangeri	39597	Clark Fork, Sand Coulee (Simpson, 1937, p. 9)
Esthonyx latidens	16066	Clark Fork, Sand Coulee (Simpson, 1937, p. 10)
Phenacodus hemiconus	16056	Gray Bull (Granger, 1915, p. 339)
Phenacodus primaevus	16054, 16059. 1 unnumbered	Clark Fork, Sand Coulee, Gray Bull (Granger, 1915), p. 354)
Thryptacodon antiquus	16075, 16076	Clark Fork, Sand Coulee, Gray Bull (Matthew, 1915a, p. 8)

as he states (1915, p. 339): "Eleven specimens from the Gray Bull beds and one from the Lost Cabin are referable to this small variety." Thus there is nothing distinctive about the specimens from this locality to suggest their association with the Clark Fork fauna; on the contrary, based on the presence of *Phenacodus hemiconus,* there is a slight suggestion that these specimens may actually be of Gray Bull derivation. At any rate, since this area was not described as one of Granger's type localities, and since its faunule does not differ significantly from those of other Sand Coulee or lower Gray Bull sites, it seems highly probable that "east" or "three miles east of Pat O'Hara Creek" is in Sand Coulee or lower Gray Bull, and not Clark Fork, strata.

Specimens from locality 3 are too vaguely labelled to be of any value in this study. Faunas from the southeastern side of Polecat Bench have been found ranging from the Silver Coulee through the lower Gray Bull. Without knowledge of section, township, and range, it is virtually impossible to infer to what fauna these American Museum fossils belong. It is very likely that elements from several faunas are actually represented by these fossils. Therefore, on the basis of the foregoing inferences, none of the American Museum materials from localities 1, 2, or 3 can certainly be ascribed to what have been regarded as Clarkforkian strata. Rather, those from localities 1 and 2 can be considered as pertaining in all probability to one or more early Eocene faunas, while specimens from locality 3 cannot be definitely assigned either to a late Paleocene or to an early Eocene fauna.

No specimens in the collection are labelled as having come from either side of the wagon road dropping into Sand Coulee Basin (area D on map). However, any such specimens would definitely be of early Eocene age.

Listed in Table I is another group of specimens that may be considered as a unit for the purposes of this review. In contrast to the previous three groups discussed, which were characterized by similarities in locality data, this fourth group is distinguished by a total lack of useful locality information. Labelled variously as coming from "Clark Fork beds" or "formation," or even "Clark Fork Period," these fossils clearly can be of no use in defining the composition of the fauna for the following reasons. First, as has already been shown, if these fossils came from localities 1, 2, or 3, they probably should not be included in the Clark Fork fauna. Second, if these specimens were not found at localities 1, 2, or 3, then they could have been picked up anywhere by

chance in a basin where four faunal horizons (Silver Coulee, Clark Fork, Sand Coulee, and Gray Bull) have been described, as the labels associated with these specimens give no guidance as to the specific area in which they were collected.

The five remaining specimens from the type collection, not excluded from being Clarkforkian by virtue of the considerations already discussed, are listed in Table I under the column headed "other." Of the fossils in this category, only two specimens, one of *Coryphodon* sp., and one of *Ectocion osbornianus ralstonensis*, were found at one of Granger's type areas, "between Little Rocky and Line Creeks," marked as locality E on the map. The hachures in section 3, T 57 N, R 102 W of Granger's field map probably represent the exposures in which these specimens were collected. Andrews, Pierce, and Eargle (1947) showed both Paleocene and Eocene sediments in this region. However, Pierce (1965) indicates that only Eocene and Quaternary deposits are found within this section. Very probably, therefore, the two specimens under consideration should be associated with the Sand Coulee or Gray Bull faunas.

Also in this last category is one specimen of *Phenacodus primaevus* that was found "6 miles north and one mile east of Powell, Wyoming, at base of bluff," unquestionably an area of Paleocene deposits. This specimen may be regarded as coming from the Polecat Bench Formation.

Accompanying a single specimen of *Probathyopsis praecursor* (AMNH 16063) are the following locality data: "southeast side of Clark's Fork, opposite mouth of Little Rocky Creek, Ralston [Clark Fork] formation." The most recent maps show Little Rocky Creek as being a tributary of Bennett Creek, and the sediments opposite its mouth, on the west side of the Clarks (or Clark) Fork River are mapped as Quaternary in age. However, Fisher's map shows Bennett Creek as being a tributary of Little Rocky Creek (see p. 8), and the rocks opposite the latter creek's mouth on the east bank of the Clarks Fork River were mapped as being of Eocene age. Therefore, it would seem that the locality designated by the label refers to the area opposite the mouth of Bennett Creek as its course is presently mapped. Hachures in this vicinity on Granger's field map (Fig. 2) would appear to confirm this deduction. Excluding the Quaternary deposits immediately to the east of the Clarks Fork channel, Jepsen (1930b), Stow (1938), Andrews, Pierce, and Eargle (1947), and Pierce (1965) have all regarded the sediments of this area as being of Paleocene age. In this review, therefore, this one specimen of *Probathyopsis* will be regarded as being from upper Paleocene beds.

In the case of the only fossil not yet discussed, the locality data are relatively specific. The type of *Oxyaena aequidens* is from "Clark Fork beds, Clark Fork Basin, 1912, about seven miles east of Pat O'Hara Creek." Rocks in this part of the Clark Fork Basin are extremely flat-lying, and it is rather difficult to establish the contact between the conformable Paleocene and Eocene strata, as can be seen from the fact that the contact lines drawn by different mappers differ markedly one from another (see Fig. 3). The *Oxyaena* specimen was probably found somewhere in this contact region. However, considering both the fact that the distance estimate made in 1912 could have been at best only an approximation, and that there is no agreement as to exactly where the contact lies in this region anyway, it can only be a matter of speculation as to whether this specimen belongs to a late Paleocene or an early Eocene fauna. Thus, the specimen is of no help in defining the Clark Fork fauna.

Of the original Clark Fork collection of 89 specimens, therefore, only two, one of *Phenacodus primaevus* and one of *Probathyopsis praecursor,* may be certainly regarded as being from the Polecat Bench Formation. The remainder of the specimens must be excluded from this category for one of two reasons. Either the fossils are of a different age from what they were originally considered to be, or the locality data associated with the specimens are not specific enough to be of any stratigraphic utility. As it would be unwarranted to try to define a fauna on the basis of only two species, each represented by only one specimen, it is necessary to analyze other evidence pertaining to this problem.

THE PRINCETON UNIVERSITY COLLECTION

Comparison of Tables I and III reveals several marked differences between the Princeton and the American Museum Clark Fork collections. First, there are only about one-fifth as many specimens in the Princeton collection as in that of the American Museum. Second, there are somewhat better documented locality data for the Princeton material. Still another contrasting factor is that the preponderance of the American Museum specimens was collected during the two field seasons of 1910 and 1911, while Princeton parties have been adding to the collection continuously for over 30 years. Only genera added to Clark Fork fauna by Jepsen in 1930 (with the exception of *Parectypodus,* see above, p. 5) will be considered in the present review, as these elements are the ones that have formed part of the basis on which the fauna has usually been defined.

TABLE III

SPECIMENS UPON WHICH PUBLISHED REPORTS OF THE PRINCETON CLARK FORK COLLECTION HAVE BEEN BASED.[1]

SPECIES	PU No.	LOCALITY DATA ASSOCIATED WITH SPECIMEN
Carpolestes dubius	13284	near mouth of Little Sand Coulee
	14853	S 12, T 54 N, R 96 W (Foster's Gulch)
Coryphodon proterus	13400	3 miles SW of Bear Creek, Carbon Co., Montana
Dipsalodon matthewi	13152	(type) S 14, T 56 N, R 101 W
	13311	east of mouth of Little Sand Coulee
Dissacus praenuntius	13295	east of mouth of Little Sand Coulee
	13309	east of mouth of Little Sand Coulee
Ectocion osbornianus ralstonensis[2]	13216	1 mile SW camp 3, 1928 expedition
	13310	east of mouth of Little Sand Coulee
	13312	east of mouth of Little Sand Coulee
	14872	S 12, T 54 N, R 96 W (Foster's Gulch)
Esthonyx sp.	13324	east of mouth of Little Sand Coulee
Phenacodus primaevus	13318	approx. 1 mile above mouth of Little Sand Coulee
	14994	S 8, T 56 N, R 99 W
Plesiadapis cookei	13293	(type) S 32, T 57 N, R 101 W
	13307	east of mouth of Little Sand Coulee
	13308	east of mouth of Little Sand Coulee
Probathyopsis sp.	13378	east of Little Sand Coulee near its mouth (same general area as No. 13293, *Plesiadapis*)
TOTAL NUMBER OF SPECIMENS:	18	

[1] Specific identifications are taken from Jepsen (1930b), and Simons (1960), and were checked against the labels in the Princeton University collection in 1962.

[2] Jepsen (1930b, p. 493) identified the specimens in the Princeton collection as *Ectocion ralstonensis*. The terminology used here has been altered to agree with Simpson's re-evaluation of the genus (1937, pp. 19-22; 1943, pp. 174-176).

Over one-half of the specimens in the Princeton collection were found in an area designated on the labels as "east of [or near] the mouth of Little Sand Coulee" (see Table III). How restricted an area this description represents is a moot point since the topography of this region offers few outstanding features to serve as convenient reference points and, as noted in the previous section, various mappers have differed in their opinions of exactly where the contact between the Paleocene and Eocene should be drawn in this region. Consequently, these fossils may represent strictly Paleocene forms, strictly Eocene forms, or some of both ages. In this case, not only a lack of accurate locality data, but also a lack of agreement as to where the contact is, hinder any useful evaluation of this part of the collection with respect to defining the Clark Fork fauna. The remainder of the specimens in the Princeton collection represent isolated finds scattered across a broad region. Nearly fifty miles separate the farthest spaced of the specimens attributed to the Clark Fork.

Representatives of two species, *Ectocion osbornianus ralstonensis* and *Phenacodus primaevus,* comprise roughly one-third of the Princeton Clark Fork collection. Both of these species are found in overlying faunal horizons. In addition, the presence of *Phenacodus* sp. and *Ectocion* sp. has been reported from the Silver Coulee faunal horizon immediately below the Clark Fork beds (Jepsen, 1930b, p. 491). Reference of most of the American Museum specimens, previously regarded as being of Clarkforkian age, to one or more of the early Eocene faunas was shown in the previous section to be virtually certain. Some aspects of the phylogeny of these species, originally reconstructed from studies of American Museum materials, have thus been deduced on the basis of erroneous stratigraphic assumptions. Restudy is required before they can be used in the definition of any fauna. Consequently, specimens of *Phenacodus* and *Ectocion* are at present of no value in helping to define a characteristic Clark Fork fauna.

The specimen originally designated as *Coryphodon* (species undetermined) by Jepsen (1930b, p. 493) has been described by Simons (1960, p. 13) as *Coryphodon proterus.* Only the type can be assuredly ascribed to this species. Definite inclusion of this specimen in the Clark Fork fauna is not possible. It was found at the foot of the Beartooth Mountains where unconformities between Tertiary and Paleozoic rocks prevent accurate determination of stratigraphic position. No other fossils were found associated with *Coryphodon proterus,* so that no faunal clues are available to help make stratigraphic inferences. In fact, the only

reason for referring this specimen to a Paleocene horizon is that it was found in rocks mapped, presumably on non-paleontological grounds, as being of Paleocene age. Whether *C. proterus* is of Paleocene or Eocene age cannot be determined on the basis of available evidence.

Similarly, the one specimen of *Esthonyx* sp. known from the Princeton collection must be excluded from further consideration as an element of the Clark Fork fauna, since it is impossible to determine whether the specimen came from Paleocene or Eocene beds (see Table III, text p. 21). However, since all the American Museum Clarkforkian representatives of this genus have been shown to be most probably of Lower Eocene derivation, it seems reasonable to assume, contrary evidence being lacking, that the Princeton *Esthonyx* is likely to be of the same age.

A single specimen recovered from the sediments "east of the mouth of Little Sand Coulee" was identified by Jepsen (1930b, p. 493) as *Probathyopsis* sp. Since its stratigraphic position remains in question (see above p. 21), it is unsuitable in helping to define any fauna. For the same reason, the two specimens of *Dissacus praenuntius* listed in Table III can not be used to distinguish between different faunal horizons.

The specimens of *Carpolestes dubius* attributed to the Clark Fork horizon have been recovered from two widely spaced localities. Although the age of the rocks at one of these localities is problematical, the other site is undoubtedly of Paleocene age. However, *Carpolestes dubius* is known from horizons both above and below the Clark Fork level (Jepsen, 1930b, p. 491; Van Houten, 1945, p. 450), the type being from the Silver Coulee faunal horizon. Thus this species is so wide-ranging through time that its presence is of no use as an indication of Clarkforkian age.

There is no reason to question that the type specimen of *Dipsalodon matthewi* was found in late Paleocene sediments. Unfortunately, the only other specimen was collected in the problematical region "east of the mouth of Little Sand Coulee." However, Patterson (personal communication) informs me that a specimen of *?Dipsalodon* sp. is present in the Plateau Valley fauna of Tiffanian age. Patterson's specimen (FMNH No. P26095) is a fragment of the right maxilla with P^4, the broken stump of M^1, and the root of M^2. It can be compared with AMNH No. 16068, consisting of P^4 and M^1, which Denison (1938, p. 175) has doubtfully referred to *D. matthewi*. (This specimen is listed as an oxyaenid in Table I.) But since Jepsen's two specimens of *D.*

matthewi are both represented by lower teeth only, no direct comparison can be made between them and Patterson's specimen. (PU No. 13152 (type) has P_{1-4}, M_{1-2}; PU No. 13311 is an M_1.) Patterson's manuscript notes state that his "specimen is smaller than the type of *D. matthewi* and AMNH No. 16068. It probably represents a new species." In spite of not being able to make direct comparisons between Patterson's and Jepsen's specimens, however, it is possible to say that they are roughly of the same size and morphology, as might be expected in forms related at the generic level. Consequently, *Dipsalodon* can no longer be regarded as the only genus restricted to the Clark Fork fauna.

Precise locality data are associated with only one of the supposedly Clarkforkian representatives of *Plesiadapis cookei* (Table III). But this specimen, the type, was found in the region east of the mouth of Little Sand Coulee where disagreements exist concerning the location of the contact between Paleocene and Eocene sediments. The specimen's uncertain stratigraphic derivation precludes its being clearly assigned either a Paleocene or an Eocene age. The two other specimens of *P. cookei* were also found in the same general area, and the same uncertainty applies to them. Thus, on the basis of published evidence it is not possible to include *P. cookei* definitely in the Clark Fork fauna.

As already stated, over half of the Princeton collection must be eliminated from consideration as elements of the Clark Fork fauna solely on the basis of insufficiently precise locality data. Because of wide-ranging stratigraphic distribution and a lack of reliable knowledge regarding phyletic relationships, other specimens are similarly not suitable for defining the fauna. Only two described specimens in the Princeton collection, the type of *Dipsalodon matthewi* and one of *Carpolestes dubius,* may still be considered as having certainly come from the latest Paleocene strata in this area. Together with one specimen of *Phenacodus primaevus* and one of *Probathyopsis praecursor* in the American Museum collection, these fossils represent the only certain components of what has been described as the Clark Fork fauna. As previously mentioned, however, *Phenacodus* is at present of no use for fine age discriminations between rocks in the mid-Paleocene to early Eocene time span. The single specimen of *Probathyopsis praecursor* can hardly be diagnostic of a latest Paleocene faunal assemblage when all the other described specimens of this species are probably of early Eocene age. *Carpolestes dubius* is already known to range from Silver Coulee to Gray Bull. Since nothing

is known about the rates of deposition of the Polecat Bench sediments, it is possible that the "Clark Fork" specimens of *Phenacodus primaevus, Dipsalodon matthewi, Carpolestes dubius* and *Probathyopsis praecursor* may be either essentially contemporaneous with or of a younger age than the fossils in the Silver Coulee fauna. But until a larger number of fossils from the latest Paleocene sediments are found, it is not possible in practice to differentiate a Clark Fork fauna from those of under- and overlying strata. At any rate, to base one of the provincial ages in the standard section of the North American Continental Tertiary on a "fauna" consisting of only four specimens representing four species seems unwarranted. As a direct consequence there also do not seem to be sufficient grounds for continuing to regard the Clark Fork as a discrete uppermost Paleocene faunal zone or as a member of the Polecat Bench Formation.[1]

SOME RELATED PROBLEMS

If it is accepted that a definitive Clark Fork fauna is not a reality, then a number of questions arise. For example, most of the American Museum material of *Probathyopsis praecursor,* including the type, clearly is from lower Gray Bull beds. In addition, there is no certainty as to whether the one specimen of *Probathyopsis* sp. was found in Paleocene or Eocene deposits. These facts complicate the evolutionary sequence proposed by Jepsen (1930a, p. 129) of (1) *P.* sp., (2) *P. praecursor,* and (3) *P. successor.* The evidence strongly suggests that *P. praecursor* and *P. successor* actually existed contemporaneously rather than that the former gave rise to the latter. Furthermore, it is entirely possible that *P.* sp. might also have coexisted with the other two forms. Wheeler (1961, p. 21) states that *P. newbilli* from the Plateau Valley beds "is quite distinct from both *P. praecursor* and *P. successor* and is not closer to one than to the other." Such a statement suggests that *P. newbilli* could be ancestral to the two later, divergent forms. However, this scheme would not clarify the relationship of *P.* sp. to the other forms with which it may have been contemporaneous. Jepsen (1930a, p. 129) felt that *P.*

[1] The possibility of course exists that a post-Tiffanian Paleocene provincial age may be recognized in the future. In that event the age would require a new name. "Clarkforkian" could be resurrected only if a real fauna of such age were to be found in the Clark Fork area. In view of the intensive search for one that has been made there over the past thirty-five years I regard this possibility as most unlikely.

sp. is more similar to *P. praecursor* than to *P. successor,* but until there is better stratigraphic control it will be difficult to resolve the problem of *Probathyopsis* taxonomy.

The classification of *Ectocion* has received attention from Granger, Simpson, and McKenna. From the material available to him, Granger (1915, pp. 348-354) described four species: *E. parvus, E. ralstonensis, E. osbornianus,* and *E. superstes.* Simpson (1937, pp. 19-22; 1943, pp. 174-176), however, felt that Granger's four species should be regarded as successive subspecies grouped under the specific name *E. osbornianus.* More recently, McKenna (1960, pp. 102-103) discussed *Ectocion* classification in his paper on the Four Mile fauna. His remark (p. 103) that "the locality data of practically all existing collections of Willwood mammals are inadequate for detailed stratigraphic (and hence evolutionary) analysis" is equally applicable to specimens attributed to the Clark Fork fauna. But neither Simpson's nor McKenna's proposed classification is clearly acceptable because of the probability that most of the American Museum's Clarkforkian specimens are of Eocene rather than Paleocene age. *E. osbornianus ralstonensis,* for example, presumably existed contemporaneously with *E. o. complens,* formerly thought to be the evolutionary successor of this species.

Restudy of early representatives of the genus *Phenacodus* will also be required. Two species, *P. primaevus* and *P. intermedius,* whose ranges were listed as extending down into Clark Fork beds, were described by Granger (1915, pp. 337, 342). Subsequently Jepsen (1930b, p. 491) reported the presence of *P.* sp. in his Silver Coulee fauna. *Phenacodus primaevus grangeri* is also known from the Plateau Valley fauna (Patterson, personal communication). Simpson (1937, pp. 17-19) published a statistical analysis of the lower Gray Bull and Clark Fork phenacodonts in the American Museum collection. He thought that possibly the Clark Fork and some of the Gray Bull specimens represented a single species. Further, he felt that perhaps the two groups might be differentiated on a subspecific level, concluding (p. 19) "that the Clark Fork specimens are a nearly or quite homogeneous sample of one subspecies and that this subspecies may also occur in the Gray Bull . . . or may be distinct. These alternatives cannot at present be adequately checked." In view of the probability that most of the supposed Clarkforkian phenacodonts were actually found in Gray Bull beds, it would not be surprising if the two samples represented only one species.

Conceivably the type and only known specimen of *Plesiadapis dubius* (AMNH No. 16073) could have come from either late Paleocene or early Eocene strata, having been found at locality

number 3. In appearance it most closely resembles *P. fodinatus,* originally described (Jepsen, 1930b, p. 515) from the late Paleocene Silver Coulee horizon. The character separating these two species was noted by Jepsen as follows: "The anterior crest of P_4 is developed into a minute cuspule, and a small ridge appears on the anterolingual part of the protoconid, quite in contrast to the distinct metaconid on P_4 of *P. dubius.*" Unfortunately, P_4 of the type of *P. fodinatus* (PU No. 13278) has been broken off and is now missing, so that it is no longer possible to make the comparison except from Jepsen's illustrations. The abundant quarry material of *P. fodinatus,* most of which has been obtained since 1930, reveals, however, that the presence or absence of a distinct metaconid is a variable feature and not a specific character. That only one specimen of *P. dubius* has ever been found seems curious, in view of the rather extensive amount of field work in the upper Paleocene and lower Eocene beds of this region. Since the range of *P. fodinatus* has been, subsequent to 1930, extended up into the lower Gray Bull by continued collecting, it appears entirely possible that *P. fodinatus* is a synonym of *P. dubius.*

The Sand Coulee beds were defined by Granger (1914, p. 205) as follows: "This horizon does not contain *Systemodon* but it does contain the Perissodactyl genus *Eohippus* in abundance as well as Artiodactyls, Rodents, and Primates, and marks the first appearance of these four orders. It also marks the last appearance of the primitive order Multituberculata which is represented in this horizon by a genus of Plagiaulacids." Many of the criteria used to characterize this faunal zone have in the past fifty years been shown not to be definitive. Rodents and primates were later found in the Paleocene. Granger's "plagiaulacids," now classified as ptilodonts, are known from levels higher than the Sand Coulee.[1] When *Homogalax* (*Systemodon*) was found in the Sand Coulee beds subsequent to Granger's definition of them, Jepsen (1930a, p. 119) suggested suppression of this term and included the beds

[1] However, multituberculates are very rare in Gray Bull and later deposits. Van Houten (1945, p. 448) reports one species, *Ectypodus simpsoni,* extending into middle Gray Bull beds. Robinson, Black, and Dawson (1964, p. 810) have described a multituberculate from upper Eocene deposits near Badwater, Wyoming. However, their specimens, representing "an undescribed species related to *Ectypodus hazeni,* . . . comprise a small percentage of the fauna, certainly less than 1 percent . . ." These two cases are the only known occurrences of multituberculates above the Sand Coulee strata.

in the Gray Bull. Simpson (1937, p. 1), however, noted that "the Sand Coulee fauna was not wholly defined . . . on the absence of *Homogalax* but also by the generally slightly less advanced character of its mammals." Now that most of the American Museum's Clarkforkian material can be probably relegated to lower Eocene beds, it may be possible to redefine a Sand Coulee fauna. For example, this might be done on the basis of the presence of *Plesiadapis cookei* and a species of *Probathyopsis,* the last abundant appearance of the multituberculates, and a more primitive aspect in those forms common to both the Sand Coulee and Gray Bull. Reappraisal of the Sand Coulee fauna is desirable in order to determine conclusively whether or not such a horizon can be distinguished.

SUMMARY

Some of the published data concerning the American Museum's Clark Fork collection do not agree with the locality information on specimen labels. For example, there are no fossils from either side of the road descending into the Sand Coulee Basin from the Bighorn Basin divide (area D), although it was described as one of the Clarkforkian type localities. The majority of the American Museum collection comes from three localities (1, 2, and 3, Fig. 3). Review shows that it is doubtful that most of these specimens from localities 1 and 2 should be referred to a late Paleocene Clark Fork horizon, but that they are rather of early Eocene age. Other specimens (those from locality 3 or labelled as being from Clark Fork "beds," "period," or "formation") are associated with such vague stratigraphic information that it is not possible to determine whether they are from upper Paleocene or lower Eocene beds. Because of insufficient locality data it is also impossible to say whether or not approximately one-half of the described Princeton collection belongs to a late Paleocene or an early Eocene fauna. A wide ranging stratigraphic distribution or a lack of adequate knowledge regarding phylogenetic relationships precludes using most of the remaining fossils to characterize the fauna.

Thus, of 107 specimens (representing at least 23 and perhaps 26 species) in both the American Museum and Princeton collections that have been described as elements of the Clark Fork fauna, a total of only four specimens representing four species (*Carpolestes dubius, Phenacodus primaevus, Probathyopsis praecursor,* and *Dipsalodon matthewi*) can be surely ascribed to a possible latest Paleocene faunal horizon in the Polecat Bench Formation. However, only one of these species (*Dipsalodon*

matthewi) may be unique to what has been described as the Clark Fork fauna. *Carpolestes dubius* is known from both the Silver Coulee and the Gray Bull. Specimens of *Phenacodus primaevus* are known from the Gray Bull, and *Phenacodus* sp. is present in the Silver Coulee. Until the phylogeny of this genus is reviewed, it is not possible to use species of *Phenacodus* for horizon markers. *Probathyopsis praecursor* is much more commonly found in early Eocene than late Paleocene beds. Thus this species can hardly be considered as diagnostic of the Clark Fork fauna. If *?Dipsalodon* sp. from the Tiffanian Plateau Valley deposits of Colorado is correctly referable to this genus, then it invalidates the supposed restriction of this genus to the Clark Fork.

Therefore, the Clark Fork "fauna" consists of four specimens referable to four mammalian genera, each from a different locality. None of the genera (and not more than one of the species) are restricted to a lithically distinguishable Clark Fork horizon. Such evidence scarcely warrants recognition of the Clark Fork as a provincial age, faunal zone, or member of the Polecat Bench Formation.

LITERATURE CITED

Andrews, D. A., W. G. Pierce, and D. H. Eargle.
1947. Geologic map of the Bighorn Basin, Wyoming and Montana, showing terrace deposits and physiographic features. Oil and Gas Investigations Preliminary Map 71.

Cope, E. D.
1874. Report on the vertebrate fossils discovered in New Mexico, with descriptions of new species. Extract from appendix FF of the Annual Report of the Chief of Engineers, 1874, Washington, Gov. Print. Office, pp. 4-18.
1880. The northern Wasatch fauna. Amer. Natur., vol. **14**, pp. 908-909.

Denison, R. H.
1938. The broad-skulled Pseudocreodi. Ann. N. Y. Acad. Sci., vol. **37**, pp. 163-256.

Fisher, C. A.
1906. Geology and water resources of the Bighorn Basin, Wyoming. U. S. Geol. Surv. Prof. Pap. No. 53, III-VI, pp. 1-72, 1 map.

Gazin, C. L.
1953. The Tillodontia: an early Tertiary order of mammals. Smithson. Misc. Coll., vol. **121**, no. 10, pp. 1-110.
1962. A further study of the lower Eocene mammalian faunas of southwestern Wyoming. Smithson. Misc. Coll., vol. **144**, no. 1, pp. 1-98.

GRANGER, W.

1914. On the names of lower Eocene faunal horizons of Wyoming and New Mexico. Bull. Amer. Mus. Nat. Hist., vol. **33**, pp. 201-207.

?1914. Annual Report of the Department of Vertebrate Paleontology, American Museum of Natural History, for the years 1911, 1912, and 1913. MS on file in the department.

1915. A revision of the lower Eocene Wasatch and Wind River faunas. Part III. Order Condylarthra, families Phenacodontidae and Meniscotheriidae. Bull. Amer. Mus. Nat. Hist., vol. **34**, pp. 329-361.

JEPSEN, G. L.

1930a. New vertebrate fossils from the lower Eocene of the Bighorn Basin, Wyoming. Proc. Amer. Phil. Soc., vol. **69**, pp. 117-131.

1930b. Stratigraphy and paleontology of the Paleocene of northeastern Park County, Wyoming. Proc. Amer. Phil. Soc., vol. **69**, pp. 463-528.

1940. Paleocene faunas of the Polecat Bench formation, Park County, Wyoming, Part I. Proc. Amer. Phil. Soc., vol. **83**, pp. 217-341.

MATTHEW, W. D.

1915a. A revision of the lower Eocene Wasatch and Wind River faunas. Part I. Order Ferae (Carnivora), suborder Creodonta. Bull. Amer. Mus. Nat. Hist., vol. **34**, pp. 4-103.

1915b. A revision of the lower Eocene Wasatch and Wind River faunas. Part II. Order Condylarthra, family Hyopsodontidae. Bull. Amer. Mus. Nat. Hist., vol. **34**, pp. 311-328.

1915c. A revision of the lower Eocene Wasatch and Wind River faunas. Part IV. Entelonychia, Primates, Insectivora (part). Bull. Amer. Mus. Nat. Hist., vol. **34**, pp. 429-483.

1918. A revision of the lower Eocene Wasatch and Wind River faunas, Part V. Insectivora (continued), Glires, Edentata. Bull. Amer. Mus. Nat. Hist., vol. **38**, pp. 565-657.

MATTHEW, W. D. and W. GRANGER.

1915. A revision of the lower Eocene Wasatch and Wind River faunas. Introduction. Bull. Amer. Mus. Nat. Hist., vol. **34**, pp. 1-4.

MCKENNA, M. C.

1960. Fossil Mammalia from the early Wasatchian Four Mile fauna, Eocene of northwest Colorado. Univ. Calif. Publ. Geol. Sci., vol. **37**, pp. 1-130.

PIERCE, W. G.

1965. Geologic Map of the Clark Quadrangle, Park County, Wyoming. U. S. Geol. Surv. Quadrangle Map GQ-477.

ROBINSON, P., C. C. BLACK, and M. R. DAWSON.

1964. Late Eocene multituberculates and other mammals from Wyoming. Science, vol. **145**, pp. 809-811.

Simons, E. L.
1960. The Paleocene Pantodonta. Trans. Amer. Phil. Soc., vol. **50,** pp. 1-98.
Simpson, G. G.
1929. A new Paleocene uintathere and molar evolution in the Amblypoda. Amer. Mus. Novit., No. **387,** pp. 1-9.
1937. Notes on the Clark Fork, Upper Paleocene fauna. Amer. Mus. Novit., No. **954,** pp. 1-24.
1943. *In* Bogert, *et al.,* Criteria for vertebrate subspecies, species, and genera. Criteria for genera, species, and subspecies in zoology and paleontology. New York Acad. Sci., vol. **44,** pp. 145-178.
1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., vol. **85,** pp. 1-350.
Sinclair, W. J., and W. Granger.
1912. Notes on the Tertiary deposits of the Bighorn Basin. Bull. Amer. Mus. Nat. Hist., vol. **31,** pp. 57-67.
Stow, M. H.
1938. Dating Cretaceous-Eocene tectonic movements in Bighorn Basin by heavy minerals. Bull. Geol. Soc. Amer., vol. **49,** pp. 731-761.
Van Houten, F. B.
1945. Review of latest Paleocene and early Eocene mammalian faunas. Jour. Paleont., vol. **19,** pp. 421-461.
Van Valen, L.
1966. Deltatheridia, a new order of mammals. Bull. Amer. Mus. Nat. Hist., vol. **132,** pp. 1-126, 8 plates.
Wheeler, W. H.
1961. Revision of the uintatheres. Bull. Peabody Mus. Nat. Hist. Yale Univ., No. **14,** iii-vi, pp. 1-93, 14 plates.
Wood, H. E., 2nd *et al.*
1941. Nomenclature and correlation of the North American continental Tertiary. Bull. Geol. Soc. Amer., vol. **52,** pp. 1-48, 1 plate.

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BIOLOGY OF THE PARTHENOGENETIC FUNGUS BEETLE *CIS FUSCIPES* MELLIÉ (COLEOPTERA: CIIDAE)

By John F. Lawrence

Thelytoky, or female-producing parthenogenesis, has been reported for a large number of animal groups, and a considerable amount has been written on its occurrence in various groups of insects, such as the Psychidae, Aphididae, Tettigoniidae, Phasmidae, and Curculionidae (White, 1954; Suomalainen, 1962). Aside from the well known cases in *Ptinus clavipes* and several European weevils, there have been few references to thelytoky in the Coleoptera; yet this type of reproduction is probably fairly common throughout the order, judging from the number of groups in which unusual sex ratios have been noted. The step from the preliminary observation to experimental evidence is often a big one, however, because of the difficulties encountered in rearing many insects. While endeavoring to straighten out a taxonomic problem concerning some small fungus-feeding beetles in the family Ciidae, I discovered an apparent case of thelytoky in the species *Cis fuscipes* Mellié, and was able to confirm this by a series of rearing experiments discussed below. To my knowledge, this is the first record of its occurrence within the large superfamily Cucujoidea.

In connection with a study on the systematics and biology of western North American Ciidae, an attempt was made to distinguish between two apparent sibling species, *Cis fuscipes* Mellié and *Cis impressus* Casey. The two species are widespread in North America, have broadly overlapping distributions, and feed on the same species of fungi. The only characters given in the literature to separate the two are the form of the male pronotum and abdomen; in *C. impressus* the pronotum of the male is impressed anteriorly and the abdomen bears a setigerous pore on the first visible sternite, while both characters are apparently absent in the "male" of *C. fuscipes*. Females of the two species are apparently indistinguishable (Casey, 1898; Dury, 1917).

In an attempt to solve this problem, I examined about 1500 museum specimens from various parts of North America, collected large series of adults and larvae from both dimorphic and monomorphic populations in California, and dissected series from California and Minnesota, in order to examine genital characters. No characters could be found to separate females or larvae of the two species, nor could any external sexual characters be found in *C. fuscipes*. When dissections were made of relatively large samples, it was found that the monomorphic series consisted entirely of females. This led to the hypothesis that thelytoky was occurring in *C. fuscipes* and that the name *impressus* had been applied to male specimens of the same species. The following rearing experiments were then conducted.

REARING EXPERIMENTS

Larvae of *Cis fuscipes* and fresh pieces of *Polyporus versicolor* were collected in Marin Co. and Alameda Co., California. Each larva was isolated in a petri dish with a piece of fungus, and water was added from time to time. Each resulting female was kept in isolation and observed periodically for the presence of eggs and larvae. Several rearings were attempted, but only one will be discussed here. One larva was isolated on December 9, 1962, and by January 26, 1963, it had pupated and eclosed, producing an adult female. By February 7, eggs had been laid and early instar larvae were seen boring in the fungus. By April 1, 15 females were seen in the medium; 7 of these were preserved, while the other 8 were isolated in separate dishes. Eggs were seen in most of these dishes by May 4, and on May 31, all the adult females were removed and preserved, leaving only the F_2 larvae in the dishes. By July 19, adult F_2 females were present in all 8 dishes. Five of the clones were preserved, and the numbers of individuals contained in each were as follows: 51, 50, 43, 42, and 47. The remaining clones produced an F_3 generation by October 24, and one of these was retained to produce F_4's by the end of the year.

Because of intermittent field work, the exact generation time could not be recorded, but the F_1 generation was produced in about 60 days, which appears to be a reasonable figure when compared with observations made on several other ciid species.

Two attempts were made to cross females from these parthenogenetic clones with males collected in the same area; all of these were unsuccessful in that only female progeny resulted. Mating probably did not take place, but many more trials will be necessary

before one can conclude that parthenogenetically-produced females will not cross with males from bisexual populations.

It is obvious that some form of thelytoky is occurring in this species, but the actual cytological mechanisms involved have not been studied. Chromosome counts made by Mr. Norihiro Ueshima showed that the diploid number is 14 both in the male and in the parthenogenetic female. Thus polyploidy does not occur in the California populations examined.

GEOGRAPHICAL AND ECOLOGICAL RANGE

Cis fuscipes is the most widespread and common species of Ciidae in North America, ranging from northern British Columbia to southern California on the Pacific Coast, east across southern Canada to Nova Scotia, and south throughout the eastern and midwestern United States (east of the 100th meridian) to Brownsville, Texas, and Dunedin, Florida (Fig. 1). It is apparently absent from the more arid parts of the continent, such as the Great Plains, the Great Basin, and the southwestern deserts. A single record from Provo, Utah, indicates its possible occurrence in the poorly collected Rocky Mountain region. Specimens have also been seen from Mexico (no specific locality), Cuba, Hawaii, and from the island of Madeira in the eastern Atlantic. These isolated records will be discussed below.

Throughout its range, the species occurs in association with several species of bracket fungi (Basidiomycetes: Polyporaceae), where both adults and larvae feed within the fruiting bodies. It appears to be restricted to members of the *Polyporus versicolor* group (Paviour-Smith, 1960), which have small, relatively thin sporophores with whitish, punky context and a trimitic hyphal system and which usually cause white rot in dead or dying angiosperms. It is especially common in *Polyporus versicolor,* which may be considered its "headquarters" (Elton, 1949; Paviour-Smith, 1960), but also feeds on related fungi. Out of the 92 host records which I have accumulated for this species, 72 are from *P. versicolor,* 7 from *P. hirsutus,* 6 from *Lenzites betulina,* 2 from *P. conchifer,* and a single record each from *P. squamosus, Trametes suaveolens, Fomes fraxineus, Ganoderma brownii,* and *P. gilvus.*

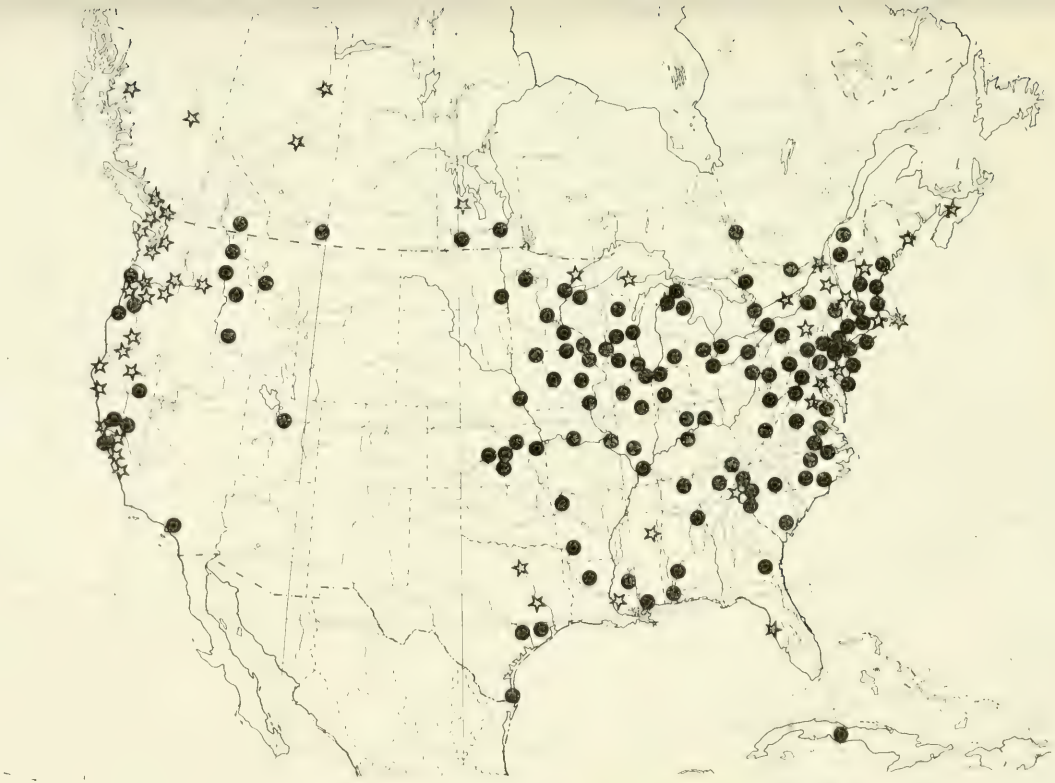
In the western part of its range, *Cis fuscipes* is usually found associated with *Cis versicolor* Casey, *Cis vitulus* Mannerheim, *Sulcacis curtulus* (Casey), *Ennearthron californicum* Casey, and *Octotemnus laevis* Casey. In California, extensive collecting has revealed that *C. fuscipes* (as well as *C. vitulus* and *O. laevis*)

requires a somewhat more humid environment than *C. versicolor, S. curtulus,* or *E. californicum,* and it may be replaced by these species in drier environments. In the eastern part of its range, the species occurs with a number of other ciids, including *Cis pistoria* Casey, *Cis falli* Blatchley, *Sulcacis lengi* Dury, *Strigocis opacicollis* Dury, and *Octotemnus laevis* Casey, and other fungivorous beetles, such as *Neomida bicornis* (Fabricius) and *Euparius marmoreus* (Oliviér). It is relatively common in most areas and appears to be successfully competing with other species inhabiting the same fungi.

Like many species of polypores, *P. versicolor* and its relatives are widely distributed and are found on many different tree species, although they are normally restricted to angiosperms. One might expect a fairly continuous distribution of these fungus species within any deciduous forest, but the actual occurrence of fruiting bodies will depend upon the forest composition, number of dead trees, and physical factors affecting the establishment of the fungus and the production of sporophores. Even in a continuous forest, one may find *P. versicolor* replaced in certain areas by *P. gilvus* or *P. pargamenus,* each of which support different ciid species. This breaking up of the habitat will be more evident, of course, where the hardwoods themselves are scattered or rare. The absence of *Cis fuscipes* from the more arid part of western North America may be due to the inability of the species to tolerate drier environments, as was suggested by observations on California populations, rather than to the lack of hardwood forests, or to physical factors affecting the host fungi. The relative rarity of the beetle in the more humid parts of the Sierran and Cordilleran ranges, however, may be related to the scattering of the habitat, since large stands of conifers separate riparion situations in which alders and other angiosperms provide a suitable medium for the host fungi.

DISTRIBUTION OF BISEXUAL POPULATIONS

The abundance of male specimens varies considerably throughout the range of this species. Since intensive population sampling was not attempted, it is not possible to present a detailed analysis of the sex ratios, but a general idea of the distribution of bisexual populations may be derived from the data recorded for over 2500 specimens (from 405 localities) collected by myself or borrowed from various museums. For the entire range, 12 per cent of the specimens examined were males, and these represented 21.7 per cent of the localities. In Figure 1, the localities from which



FIGURE

Map of the New World distribution of *Cis fuscipes* Mellié. Black circles represent localities from which only females have been recorded; stars indicate the presence of at least one male in the series.

males were taken are represented by stars, while those from which only females were recorded are represented by black dots. Two things that are immediately apparent are: 1) the preponderance of male records in the northwestern part of the continent, as compared to their rarity on the east coast and complete absence in the Midwest, and 2) the scattered occurrence of males throughout the range as far south as Florida and Texas. From California, Oregon, Washington, British Columbia, and Alberta, 918 specimens (36.2%) from 77 localities (19.0%) were examined, and of these 221 specimens (24.1%) from 51 localities (66.2%) were males. From the remainder of Canada and the United States, 1618 specimens (63.8%) from 328 localities (81.0%) were examined, and of these 84 specimens (5.2%) from 37 localities (12.7%) were males. Of the total male specimens examined, 72.4 per cent were collected in the Pacific states and western provinces.

Although the sample sizes vary greatly and were often small, (decreasing the reliability of negative evidence), I think there is little doubt that bisexual populations are more abundant in the Northwest and become increasingly rare to the east and south. Parthenogenetic populations occur throughout the range, and in northern coastal California both types appear to be common in any one area. Males have been taken at several localities along the east coast and in the Gulf Coast states, but I have seen no records of their occurrence in the Midwest.

SYSTEMATIC RELATIONSHIPS AND PROBABLE ORIGIN

Cis fuscipes is closely related to a group of Old World species which were placed in the subgenus *Hadraule* Thomson by Reitter (1902), Chujo (1939), Miyatake (1954), and others. The name *Hadraule,* however, does not apply to the group, since its type species, *Cis elongatulus* Gyllenhal, has been excluded (Lohse, 1964; Lawrence, 1965). The species seem to form a natural unit and are characterized as follows: stout, oblong to subparallel body form; pronotum with fairly broad lateral margins and produced and rounded apical angles, which are preceded by a lateral inflexion of the disc; dual and subseriate elytral punctation; vestiture of stout, erect bristles; prosternum slightly tumid but not carinate; apex of the protibia strongly dentate; and the male with two weakly developed clypeal plates, anteriorly impressed pronotum, setigerous pore on the third abdominal sternite, and relatively simple aedeagus. The species group extends from eastern

Siberia through southeastern Asia and India to Africa and Madagascar, being absent in northern Africa and Europe, but the species which most closely resemble *C. fuscipes* occur mainly in Siberia and Japan. These include *Cis seriatopilosus* Motschulsky (Siberia: Amur, Sakhalin; Japan); *Cis seriatulus* Kiesenwetter (Japan); *Cis heiroglyphicus* Reitter (Siberia: Khabarovsk; Japan); *Cis taiwanus* Chujo (Taiwan, Loo Choo Islands, Japan?); *Cis subrobustus* Miyatake (Japan); and *Cis japonicus* Nobuchi (Japan).

Those species which have been studied biologically occur on the same fungi as *C. fuscipes. Cis seriatopilosus* and *C. taiwanus* have both been recorded from *Polyporus versicolor,* while *C. subrobustus* has been collected on *P. hirsutus* (Chujo, 1939; Fukuda, 1940; Miyatake, 1954). Although most of these beetles appear to be specifically distinct from the North American species, a single Siberian specimen identified by Reitter as *C. seriatopilosus* is very similar to individuals of *C. fuscipes.* Perhaps further collecting in eastern Siberia will reveal the presence of *fuscipes* there.

The presence of several close relatives in Asia and the abundance of males in the northwestern part of the range suggest that *Cis fuscipes* or its ancestor dispersed into North America across the Bering Strait from a point of origin in the eastern Palaearctic. Since there is no evidence of unusual sex ratios among the Japanese and Siberian species, it is probable that the parthenogenetic mode of reproduction originated in northwestern North America and the species subsequently spread east and south across most of the continent.

In the absence of a fossil record, there is no direct evidence relating to the time of dispersal of *C. fuscipes* into North America. Some indirect support may be derived from Linsley's analysis of the cerambycid beetle fauna (1958), in which he considers all of the northern or Holarctic elements of the fauna to be post-Pleistocene in origin. Several of the examples of thelytoky in animals have been demonstrated to be glacial phenomena; this is discussed by Suomalainen (1962) for insects, and by Darewski and Kulikova (1961) for lacertid lizards. The recent origin of parthenogenesis has been argued by some authors on theoretical grounds, because of the inherent long-term disadvantages of this type of genetic system.

SPREAD AND OVERSEAS DISPERSAL

The ability of a parthenogenetic species to colonize and spread rapidly throughout a new area is well known and has been discussed in various texts, such as White (1954), and Mayr (1963).

A system which suspends sexual reproduction not only makes possible the perpetuation of a successful genotype as soon as it is formed, but doubles the fecundity by eliminating the "reproductive wastage" characteristic of a population in which roughly half of the individuals are males. Where the suitable habitat for a species is broken up, a parthenogenetic form will be able to spread more rapidly, since only a single female need reach a favorable microenvironment. In an area which is initially unsuitable for a bisexual species, the development of a parthenogenetic system may speed up the process of adaptation to the new environment by immediately fixing and reproducing a favorable genotype. Stebbins (1950) and others have stressed the importance of apomixis in the rapid colonization of new habitats by plant species.

A comparison of the ranges of North American Ciidae shows that only *Cis fuscipes* occurs throughout the northern part of the continent and yet is also an important element in the fauna of the southeastern and midwestern United States. Several other species have northern distributions and similar affinities to Palaearctic species. Some of these, such as *Cis horridulus* Casey and *Dolichocis indistinctus* Hatch extend southward only in montane regions and may occur in the southern Appalachians or in the mountains of Arizona. *Sulcacis curtulus* (Casey) extends into southern California but is rare in the northeastern and northern midwestern states. *Eridaulus levettei* (Casey) is fairly widespread in the eastern part of the continent, but does not occur in the West, while *Octotemnus laevis* Casey is common along both coasts and in parts of the Midwest. Neither of these species is as common or widespread as *C. fuscipes,* and both are absent from the Southern Coastal Plain and Gulf Coast. Two other wide-ranging species, *Ennearthron californicum* Casey and *Ennearthron thoracicorne* (Ziegler), occur in the western and eastern states respectively. Both of these, however, are of southern origin, having their closest relatives in the Neotropical Region, and neither extends far into Canada. The comparison of *C. fuscipes* with other northern or Holarctic members of the North American fauna may seem to imply that all of these have similar relationships to Palaearctic species and thus represent Old World invasions of roughly the same age. This does not appear to be the case. All of the other northern species have Old World counterparts which extend throughout the Palaearctic from Europe to Siberia and Japan, whereas only *C. fuscipes* belongs to a group restricted to the eastern Palaearctic and Oriental regions and having some relationships with palaeotropical forms. It may be that *C. fuscipes*

represents the most recent element in our fauna, but there is no direct evidence for this.

I think there is little doubt that the evolution of thelytoky in *C. fuscipes* is responsible for the apparently rapid spread of the species and for its present wide distribution in North America. In addition to the obvious advantages of the parthenogenetic system to dispersal and colonization, the increased fecundity has probably contributed to its success in competing with the large and diverse fauna of southern origin occupying the southern periphery of the range. The only large area in North America which is suitable for *C. fuscipes,* but in which the forest cover is considerably broken up, due partly to agriculture, is the Midwest. It is interesting that this is the only region in which males are totally absent.

The presence of males in scattered localities along the east coast and at the southern extremities of the range raises several questions which can be answered only by more detailed population studies. Is the parthenogenetic form the result of a single evolutionary event, an obligate thelytokous form being completely independent of the bisexual form? Is a residual bisexual population continually giving rise to parthenogenetic clones? Is parthenogenesis facultative in this species, so that occasional females can give rise to normal males? It is hoped that future studies will provide the answers.

Mellié's original series of *Cis fuscipes* included several specimens from the island of Madeira. It would seem improbable that the Madeiran series represents the same species, but an examination of Mellié's and Wollaston's specimens revealed that they are conspecific with the North American *fuscipes,* and that they are all females. According to Wollaston (1854, 1865), the species has become well established in cultivated areas at low elevations around Funchal and is likely to be an accidental introduction. Although it is possible that a specimen of *fuscipes* could have rafted from the Caribbean to Madeira, it is more reasonable to assume that the species was introduced by man.

Recently, a series of female specimens of *fuscipes* were collected at Olinda on the island of Maui, Hawaii, and presented to the Commonwealth Institute of Entomology. Although Perkins, Swezey, and others have collected extensively in Hawaii, this is the first record of this species there, and probably represents a recent human introduction. In addition to this, two female specimens in the Reitter collection were apparently collected in Cuba. Whether by natural means or by human transport, *Cis fuscipes*

has dispersed from North America to these various islands, and has become established on at least one of them. The advantages of parthenogenesis in the establishment of a species having been introduced into a new area by long-distance dispersal have been discussed by several authors, including Longhurst (1955) for Crustacea, and Baker (1955) for plants.

TAXONOMIC STATUS

Because of its variability and wide distribution, *Cis fuscipes* has been given a number of names by different authors. Mellié (1848) described the species from a series of 5 specimens from Boston in the Chevrolat collection and 4 more collected by Wollaston on Madeira. In the same paper, three other names were applied to the species: *Cis atripennis,* also from Boston, *Cis chevrolatii* from "Nouvelle-Orleans," and *Cis dubius* from the latter locality. Leconte, Horn, and others applied the name *fuscipes* to the common North American species, and it has been used consistently by later authors. Casey (1898) described two more species, *Cis carolinae* (North Carolina) and *Cis pallens* (Montana), which were distinguished from *fuscipes* on the basis of color and relative lengths of antennal segments. He also described a third species, *Cis impressus* (Pacific Coast), differing from *fuscipes* only in the form of the male pronotum, which was said to be "broadly impressed at apex." Dury (1917) noted that *Cis fuscipes* occurred throughout North America, that *C. impressus* occurred on both coasts, and that the females of the two species could not be distinguished from one another. He also considered *chevrolatii* and *carolinae* to be synonyms of *fuscipes.*

During the summer of 1963, I examined the Casey types at the United States National Museum, Washington, D. C., and in the spring of 1966 I had the opportunity to study the types of Mellié in the Sallé and Pic collections at the Muséum National d'Histoire Naturelle, Paris, and in the Wollaston collection at the British Museum (Natural History), London. All of the above names, with the exception of *Cis impressus* Casey, are based on female specimens of the variable *Cis fuscipes.* The name *fuscipes* is here selected as the senior synonym because of its continual usage in the North American literature. Being based on a bisexual population, Casey's name *impressus* presents certain difficulties. Since it has not yet been established whether this species is facultatively parthenogenetic or rather composed of a bisexual species and one or several obligate parthenogenetic clones, it could be

argued that the name *impressus* should be applied to populations in which males occur. The true nature of the biological situation will be made clear only after intensive population analyses, rearing experiments, and cytological studies. In any case, I prefer to consider *impressus* a synonym of *fuscipes* on purely practical grounds, since no characters have been found to distinguish the larvae or females of the two forms. I therefore propose the following synonymy:

Cis fuscipes Mellié

Cis fuscipes Mellié, 1848: 271, pl. 2, fig. 23; Wollaston, 1854: 281; Wollaston, 1865: 234; Casey, 1898: 78; Blatchley, 1910: 898; Dalla Torre, 1911: 11; Dury, 1917: 11; Leng, 1920: 246; Weiss, 1920: 138 (host); Weiss and West, 1920: 8 (host); Weiss and West, 1921b: 169 (host); Böving and Craighead, 1931: 270-71, pl. 92, figs. K-R (larva); Arnett, 1962: 827, fig. 1.98; Hatch, 1962: 231; Lawrence, 1965: 279. Type locality: "Boston." Lectotype, female, Pic collection, Mus. Natl. Hist. Nat., Paris.

Cis atripennis Mellié, 1848: 258, pl. 2, fig. 15; Casey, 1898: 77; Dalla Torre, 1911: 6; Leng, 1920: 246. Type locality: "Boston." Holotype, female, Pic collection, Mus. Natl. Hist. Nat., Paris. NEW SYNONYMY.

Cis chevrolatii Mellié, 1848: 249; Blatchley, 1910: 898; Dalla Torre, 1911: 8; Dury, 1917: 11; Leng, 1920: 246. Type locality: "Nouvelle-Orleans." Lectotype, female, Pic collection, Mus. Natl. Hist. Nat., Paris.

Cis dubius Mellié, 1848: 273; Dalla Torre, 1911: 10; Leng, 1920: 247. Type locality: "Nouvelle-Orleans." Lectotype, female, Salle collection, Mus. Natl. Hist. Nat., Paris. NEW SYNONYMY.

Cis carolinae Casey, 1898: 78; Dalla Torre, 1911: 8; Dury, 1917: 11; Leng, 1920: 246. Type locality: "North Carolina (Asheville)." Holotype, female, Casey collection, U.S. Nat. Mus., Washington, D.C.

Cis impressa Casey, 1898: 79; Dalla Torre, 1911: 12; Dury, 1917: 11; Blatchley, 1918: 54; Leng, 1920: 246; Weiss and West, 1921a: 61 (host); Blatchley, 1923: 19; Hatch, 1962: 231. Type locality: "Vancouver Island." Holotype, male, Casey collection, U. S. Nat. Mus., Washington, D. C. NEW SYNONYMY.

Cis pallens Casey, 1898: 78; Dalla Torre, 1911: 15; Leng, 1920: 246. Type locality: "Montana (Missoula)." Holotype, female, Casey collection, U. S. Nat. Mus., Washington, D. C. NEW SYNONYMY.

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LITERATURE CITED

ARNETT, R. H.

1962. The beetles of the United States (A manual for identification). Part V. Fascicle 98. Cisidae. Catholic Univ. Amer. Press, Washington, D. C. Pp. 827-830, pl. 1.98.

BAKER, H. G.

1955. Self-compatibility and establishment after "long-distance" dispersal. Evolution, 9(3): 347-348.

BLATCHLEY, W. S.

1910. An illustrated descriptive catalogue of the Coleoptera or beetles (exclusive of the Rhynchophora) known to occur in Indiana. Bull. Indiana Dept. Geol. Nat. Res., **1**, 1385 pp., 590 figs.

1918. On some new or noteworthy Coleoptera from the west coast of Florida. — IV. Canad. Ent., **50**: 52-59.

1923. Notes on the Coleoptera of southern Florida with descriptions of new species. Canad. Ent., **55**: 13-20, 30-36.

Böving, A. G. and F. C. Craighead
1931. An illustrated synopsis of the principal larval forms of the order Coleoptera. [part] Entom. Amer., N.S., **11**(4): 258-351, pls. 86-125.

Casey, T. L.
1898. Studies in the Ptinidae, Cioidae, and Sphindidae of America. New York Ent. Soc., **6**(2): 61-93.

Chujo, M.
1939. On the Japanese Ciidae (Coleoptera). Mushi, **12**(1): 1-10.

Dalla Torre, K. W. von
1911. Cioidae. Pars 30. *In* W. Junk and S. Schenkling, edit., Coleopterorum Catalogus. Junk, Berlin. 32 pp.

Darewski, I. S. and W. N. Kulikowa
1961. Natürliche Parthenogenese in der polymorphen Gruppe der kaukasischen Felseidechse (*Lacerta saxicola* Eversmann). Zool. Jahrbuch., **89**(1): 119-176, 35 figs.

Dury, C.
1917. Synopsis of the coleopterous family Cisidae (Cioidae) of America north of Mexico. J. Cincinnati Soc. Nat. Hist., **22**(2): 1-27.

Elton, C.
1949. Population interspersion: an essay on animal community patterns. J. Ecol., **37**: 1-23.

Fukuda, A.
1940. A study of the Japanese Ciidae, Coleoptera (II). [In Japanese] Trans. Nat. Hist. Soc. Formosa, **30**: 48-53, 5 figs.

Hatch, M. H.
1962. The beetles of the Pacific Northwest. Part III: Pselaphidae and Diversicornia I. Univ. Washington Press, Seattle. ix + 503 pp., 66 pls.

Lawrence, J. F.
1965. Comments on some recent changes in the classification of the Ciidae (Coleoptera). Bull. Mus. Comp. Zool., **133**(5): 273-293.

Leng, C. W.
1920. Catalogue of the Coleoptera of America north of Mexico. Sherman, Mount Vernon, N. Y. x + 470 pp.

Linsley, E. G.
1958. Geographical origins and phylogenetic affinities of the cerambycid beetle fauna of western North America. *In* C. L. Hubbs, edit., Zoogeography. Amer. Assoc. Adv. Sci., Publ. **51.** Pp. 299-320.

Lohse, G. A.
1964. Die in Mitteleuropa vertretenen Gattungen der Cisidae. (1. Beitrag zur Kenntniss der mitteleuropaischen Cisidae.) Ent. Blätter, **60**(2): 116-122.

Longhurst, A. R.
1955. Evolution in the Notostraca. Evolution, **9**: 84-86.
Mayr, E.
1963. Animal species and evolution. Harvard Univ. Press, Cambridge, Mass. xiv + 797 pp.
Mellié, J.
1848. Monographie de l'ancien genre *Cis* des auteurs. Ann. Soc. Ent. France, Ser. 2, 6: 205-274,313-396, pls. 9-12.
Miyatake, M.
1954. Studies on the Japanese Ciidae, I (Coleoptera). Sci. Rep. Matsuyama Agr. Coll., **14**: 40-67, 11 pls.
Paviour-Smith, Kitty
1960. The fruiting-bodies of macrofungi as habitats for beetles of the family Ciidae (Coleoptera). Oikos, **11**(1): 43-71, 1 pl.
Reitter, E.
1902. Analytische Uebersicht der palaearctischen Gattungen und Arten der Coleopteren-Familien: Byrrhidae (Anobiidae) und Cioidae. Verh. Naturforsch. Ver. Brünn, **40**: 1-61.
Stebbins, G. L.
1950. Variation and evolution in plants. Columbia Univ. Press, New York. xix + 643 pp.
Suomalainen, E.
1962. Significance of parthenogenesis in the evolution of insects. Ann. Rev. Ent., **7**: 349-366.
Weiss, H. B
1920. Coleoptera associated with *Polyporus versicolor* L. in New Jersey. Psyche, **27**: 137-139.
Weiss, H. B. and E. West
1920. Fungous insects and their hosts. Proc. Biol. Soc. Washington, **33**: 1-20, 1 pl.
1921a. Additional fungous insects and their hosts. Proc. Biol. Soc. Washington, **34**: 59-62.
1921b. Additional notes on fungous insects. Proc. Biol. Soc. Washington, **34**: 167-172, 1 pl.
White, M. J. D.
1954. Animal cytology and evolution. 2d ed. Cambridge Univ. Press. 454 pp.
Wollaston, T. V.
1854. Insecta Maderensia; being an account of the insects of the islands of the Madeiran group. Van Voorst, London. xliii + 634 pp., 13 pls.
1865. Coleoptera Atlantidum, being an enumeration of the coleopterous insects of the Madeiras, Salvages, and Canaries. Van Voorst, London. xlvii + 526 pp., appendix, 140 pp.

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EXPANDING THE PALPI OF MALE SPIDERS[1]

By William A. Shear[2]

INTRODUCTION

Genitalia and secondary sexual structures are important in the determination of spiders to the species level. This is especially true in the male, where the palpus has become modified as an intromittent organ. In many genera, the females are virtually inseparable into species, and small differences in shape, size, relative position, and complexity of the parts of the highly modified and specialized male palpus are used to distinguish between closely related species of a genus.

In families where the male palpus is highly specialized, the palpal organ has become so folded and convoluted that some parts are hidden in the normal retracted palpus. While these parts are not always of taxonomic importance, they nevertheless need to be examined in detail, especially in characterizing new species.

Many publications concerned with spider taxonomy include figures of male palpi that have been treated in order to unfold or to expand the organ. In other publications, figures are of untreated and unexpanded palpi and, as a result, confusion and uncertainty arise in comparing species and in making identifications, because frequently there are striking differences between expanded and unexpanded palpi of the same species. In an expanded palpus, sclerites, which are hidden in an unexpanded palpus, are revealed and the serial relationship of the sclerites becomes more apparent.

My purpose is not to decide what parts of the palpus are of value in taxonomy, but merely to determine what additional parts can be seen when the palpi of representative species are expanded.

[1] Part of a thesis submitted to the faculty of the University of New Mexico for the degree of Master of Science

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METHODS

In *The Spider Book,* Comstock (1940, p. 111) described a process for expanding the complex palpal organs of male spiders. This method was probably the one used by Comstock in preparing specimens for a 1910 paper on spider palpi, because the text of the 1910 publication is the same as the section on palpi in *The Spider Book.* The method he described involves immersing the palpus in boiling 10 per cent "caustic" for 10-15 minutes. After treatment, the palpus is rinsed in water and preserved in glycerine.

Engelhardt (1910) challenged this method on the grounds that the boiling solution was somewhat destructive. He was working on the more delicate female genitalia at that time. In 1925, Petrunkevitch, in a similar study, concluded that Engelhardt's objections were not substantiated by results, and further stated that palpi prepared by boiling corresponded closely to those he observed in actual use by the male spider.

Gering (1953) prepared a large series of palpi using boiling potassium hydroxide solution, but for studies of the natural mode of expansion placed preserved palpi in concentrated potassium hydroxide solution for a few minutes before a rapid transfer to distilled water, where the palpi were inflated by osmotic pressure.

Levi (1961) used hot sodium hydroxide solution, followed by distilled water. Osmotic pressure expanded the organ. In 1965, he suggested the use of boiling 85 per cent lactic acid solution, on the grounds that it is far less destructive than sodium hydroxide solution. He also mentioned that satisfactory results can be obtained by using fine needles and forceps to expand the parts of the palpal tarsus.

The method used in this study was similar to that used by Gering (1953) and Levi (1961). Palpi removed from specimens preserved in 70 per cent ethanol solution were placed in 10 per cent KOH solution for 6-8 hours at room temperature and were completely expanded in distilled water. The expanded palpi were then returned to alcohol.

Twenty-nine species, distributed among 22 genera and 10 families of higher spiders, were selected as test samples on the basis of the number of specimens available, completeness of taxonomic definition, and number of available references. Also, each of these species has palpi similar in degree of complexity to the palpi of a number of other species and genera in their respective families.

Before expanding the palpus of one of the species, a number was assigned and placed in the vial containing the specimens. In most cases, the right palpus of an individual was removed and treated, leaving the left as a control, but in some small species, the whole male was treated to avoid damage to the palpus in removal. After expansion, the palpus (or the whole specimen) was placed in alcohol in a separate vial and labelled with the same number as was previously assigned. The vial containing the palpus was then bound to the original vial of specimens with a rubber band. These specimens in alcohol were used in making the freehand drawings and in writing the descriptions.

TERMINOLOGY

The course taken by the evolution of secondary sexual structures in spiders is open to speculation. Comstock (1940), Barrows (1925), Savory (1928), Gertsch (1949), Alexander and Ewer (1957), and Levi (1961) have expressed ideas on the subject. Until we can be reasonably certain of the phylogeny of the sclerites of the male palpus, names applied to these sclerites do not necessarily indicate homologies.

Comstock (1940) effectively reviewed previous research on spider palpi and devised a system of terminology widely accepted by most authors. Comstock's terminology will be followed in this study.

The following description refers to the expanded palpus of *Araneus sericatus* (Clerck) (Figs. 20, 21).

The segments of the palpus proximal to the tarsus are only rarely modified. In most spiders, the coxa of the palpus bears an endite that functions as a mouth part, crushing and straining food material. The trochanter can bear a small projection of unknown

function. The femur of the palpus of a male spider is sometimes furnished with sclerotic picks, which rub against stridulating areas on the sides of the chelicerae, producing squeaking or barking noises. Gering (1953) demonstrated in the genus *Agelenopsis* that apophyses on the tibia and patella can serve as locking devices in copulation.

It is the palpal tarsus, especially the tarsal claw, that has been strongly modified (Barrows, 1925). The body of the tarsus has become modified in males of the more specialized families to form a cup-shaped cymbium (*cy*), the cavity of which is the alveolus. The cymbium is basal in position and the palpal organ itself folds into the alveolus when at rest (Figs. 18, 19). The most proximal portion of the organ is called the basal division. Actually attached to the wall of the alveolus is a hollow, bladder-like structure termed the basal hematodocha (*bh*). The cavity of the basal hematodocha is continuous with that of the cymbium, allowing the hematodocha to be inflated by increasing blood pressure. At the distal end of the basal hematodocha is a smooth or annulated ring of sclerotic material, the subtegulum (*st*).

The middle division consists of the tegulum (*t*), an inappropriately named ring of heavily sclerotized tissue connected to the subtegulum by the middle hematodocha (*mh*). Articulated with the tegulum is a usually small sclerite, the median apophysis (*ma*). In some male spiders, this appears as a knob or process on the tegulum.

The apical division is the most complex of the three divisions. The embolus (*e*) is the functional part of the organ, bearing at its tip the opening of the ejaculatory duct. The conductor (*c*) is a usually membranous outgrowth from the base of the embolus, serving to protect the embolus. The radix (*r*) and stipes (*s*) are small, and are often absent in less complex palpi. Both radix and stipes arise near the base of the embolus, although they may appear more distal. The palpal organs in some families do have parts of the organ actually distal to the embolus. These parts include a distal hematodocha (*dh*) and the lateral subterminal apophysis (*lsa*). The terminal apophysis (*ta*) is located at the very tip of the organ.

OBSERVATIONS

Order ARANEAE
Family THERIDIIDAE

The theridiids, or comb-footed spiders, have recently been the subject of an extensive revision by Levi from 1952 to 1964. In

1961, Levi published his ideas on the evolution of the palpal organ in this large and complex family, and concluded that the original type of palpus was probably simple, that most members of the Theridiidae have a complex palpal organ, and that secondary simplification can be seen in some otherwise highly specialized theridiids.

For my purposes, I selected four species that represent various degrees of complexity within the family.

Steatoda borealis (Hentz)

Figs. 1, 2, 3

Levi (1957a) gives excellent figures of the palpus of *Steatoda borealis* in his revision of the genus *Steatoda.* Both expanded and unexpanded palpi are shown, and some individual sclerites are figured.

In a mesal view of the unexpanded right palpus (Fig. 1), the embolus (*e*) can be seen, but the basal portion is hidden. The conductor (*c*), and the radix (*r*), both of which support the embolus in this species, are fairly obvious, but the shape of the radix is obscured by other sclerites lying over its ectal part. In a mesal view of an expanded right palpus (Fig. 2), the rotate base of the embolus (*e*) is exposed, and its true relationship to the conductor and radix (*r*) is revealed. In an ectal view of the same palpus (Fig. 3), expansion has caused a general ectad rotation of all the sclerites, bringing the median apophysis (*ma*) from behind overlying sclerites.

Enoplognatha tecta (Keyserling)

Figs. 4, 5

When Levi (1957b) revised the genus *Enoplognatha,* he gave two figures of an unexpanded palpus and one of an expanded palpus of this species.

In an ectal view of an unexpanded left palpus (Fig. 4), the median apophysis and subtegulum are completely covered by overlying sclerites, although the shape of the embolus (*e*) and its relationship to the conductor (*c*) and radix (*r*) are obvious. In an ectal view of an expanded palpus (Fig. 5), the median apophysis (*ma*) has been rotated ectad and ventrad and the subtegulum (*st*) is visible. In both Figures 4 and 5, the hooklike projection of the anterior portion of the cymbium (*cy*) is seen. This is the paracymbial hook, which in some families is developed as a separate sclerite.

Theridion differens Emerton
Figs. 6, 7

Levi (1957b) reviewed the genus *Theridion,* a very large and geographically widespread assemblage of, in many cases, remarkably similar species. Levi did not figure an expanded palpus of *Theridion differens,* although he figured expanded palpi of several other species of the genus.

When an unexpanded right palpus in ventral view (Fig. 6) is compared with an expanded right palpus (Fig. 7) seen from the same aspect, it is clear that little more is visible after expansion.

Theridion frondeum Hentz
Figs. 8, 9

This species is figured by Levi in his revision of *Theridion* (1957b). As in *Theridion differens,* an expanded palpus (Fig. 9) shows very little that is not readily visible in the unexpanded palpus (Fig. 8).

Family LINYPHIIDAE

Recent literature on this family has been restricted to a few occasional papers describing new species and giving new distributional records (Chamberlin and Ivie, 1943; Gertsch and Davis, 1946; Gertsch, 1951; and others). Blauvelt (1936) studied the palpus of *Linyphia.*

Because the palpi of members of this family are somewhat uniformly complex, two of the more common species were selected for this study.

Drapetisca alteranda Chamberlin
Figs. 10, 11

In a mesal view of an unexpanded right palpus (Fig. 10) of *Drapetisca alteranda,* the paracymbium (*pc*) is seen as a free sclerite, loosely articulated with the cymbium (*cy*). The lateral subterminal apophysis (*lsa*) is highly developed and forms a shield covering the entire palpal organ. In a mesal view of an expanded right palpus (Fig. 11), the general ectad rotation caused by expansion is readily noticed. Parts, including the subtegulum (*st*) and tegulum (*t*), which were completely hidden before treatment, are now easily seen. The bulky base of the embolus (*e*) is now visible, and the shape of the lateral subterminal apophysis (*lsa*) is more satisfactorily observed.

Linyphia marginata C. L. Koch
Figs. 12, 13

In this species, studied by Blauvelt (1936), the lateral subterminal apophysis (*lsa*), as seen in an ectal view of the unexpanded right palpus (Fig. 12), is not so highly developed as it is in the complex shield of *Drapetisca*. The tegulum (*t*) and subtegulum (*st*) are at least partially visible, but the conductor (*c*) and embolus (*e*) are obscured. In an ectal view of an expanded right palpus (Fig. 13), an ectad rotation brings into clearer view the position of the median apophysis (*ma*), which seems much more distal in the unexpanded palpus, and the exact shape and size of the unusually heavy embolus (*e*). The conductor (*c*) is readily observed, with its supporting sclerotic bar along one side. The lateral subterminal apophysis (*lsa*) is reflexed, appearing as if it were proximal, rather than distal, to the embolus.

Family MICRYPHANTIDAE

This family has not been studied as a unit since the publication of a long series of papers by Crosby, Crosby and Bishop, and Bishop and Crosby from 1905 to 1938 (listed by Kaston, 1948). Because of the seemingly simplified structure of the male palpus, there is some controversy about the proper taxonomic position of the Micryphantidae. The family is such a large one and shows so many degrees of palpal complexity that it would be impossible to treat the Micryphantidae satisfactorily in a paper of this nature. A recent study by Merrett (1963) of the palpal anatomy of this family treats the Micryphantidae as the subfamily Erigoninae of the Linyphiidae, but Merrett's work was confined to British species.

The species I studied were selected on the basis of their intermediate type of palpal organ.

Soulgas corticarius (Emerton)
Figs. 14, 15

This species was treated by Crosby and Bishop (1936), who gave a figure of an unexpanded palp, along with the characteristic cephalic modification found in this group.

An ectal view of an unexpanded right palpus (Fig. 14) shows the obviously simple structure, including a free paracymbium (*pc*), subtegulum (*st*), tegulum (*t*), and embolus (*e*). The shape of the tibia (*ti*) is unusual, having a modification that in at least some degree occurs in all male micryphantids. In mesal view, an

expanded right palpus (Fig. 15 shows two features that cannot be seen in an unexpanded palpus. The great development of the basal hematodocha (*bh*) is obvious. A small sclerite (*ma*) possibly represents a rudimentary median apophysis.

Ceratinopsidis formosa (Banks)
Figs. 16, 17

Bishop and Crosby (1930) published a figure of the unexpanded palpus of *Ceratinopsidis formosa*. The unexpanded palpus (Fig. 16) has features similar to those of *Soulgas corticarius*. In an expanded palpus (Fig. 17) observed in dorsoectal view, the greatly developed basal hematodocha (*bh*) is seen, but no sclerite corresponding to a median apophysis is apparent.

Family ARANEIDAE

Archer (1951, p. 3) defined this family as follows:

"Paracymbium vertical or divergent from the axis of the cymbium, but its basal face not resting on the apical face of the tibia, instead usually being separated from it by a distinct gap. Attachment of the genital bulb to the cymbium ranging from universal-median and then by all degrees of migration to frankly basal (as in the Theridiidae). Tegulum greatly overbalancing the subtegulum, the latter ranging from ring-like to a vestigial knob. Position of the cymbium and genital bulb normal."

If the Araneidae are considered in the strict sense, excluding the Tetragnathidae and the Theridiosomatidae, then all members of the family have complex palpi, but some do show various degrees of reduction in certain sclerites. I selected eight fairly representative species.

Araneus sericatus Clerck
Figs. 18, 19, 20, 21

The complicated palpus of this species was described in the section on TERMINOLOGY. In a ventral view of the unexpanded right palpus (Fig. 18), little can be seen except the subtegulum (*st*), tegulum (*t*), terminal apophysis (*ta*), and median apophysis (*ma*). In mesal view (Fig. 19), some additional structures are visible, but their relationships to definitely identifiable structures are obscure. A number of interesting structures are revealed in an ectal view of an expanded right palpus (Fig. 20). The anterior portion of the subtegulum is completely unsclerotized, so that the basal and middle hematodochae (*bh, mh*) are

fused anteriorly. The tegulum (*t*) is a heavy rounded structure articulating closely with the large median apophysis (*ma*). The parts of the embolic subdivision are visible distal to the tegulum. The spatulate stipes (*s*) and small conductor (*c*) articulate with the base of the embolus (*e*), but the radix (*r*) has been displaced proximad. In a mesal view of the same palpus (Fig. 21). the hook-like lateral subterminal apophysis (*lsa*) is fused with the large plate of the terminal apophysis (*ta*), and both are separated from the embolic subdivision by the distal hematodocha (*dh*).

Araneus nordmanni (Thorell)

The palpus of *Araneus nordmanni* is very similar in general plan to that of *Araneus sericatus,* differing only in the shape and position of some of the sclerites. Expansion in this species has the same effect as expansion has on the palpus of *Araneus sericatus.*

Argiope trifasciata (Forskål)
Figs. 22, 23

The main difference between the palpus of this species and those of species of the genus *Araneus* lies in the reduction of some of the sclerites of the embolic subdivision.

In a mesal view of an unexpanded right palpus (Fig. 22), the subtegulum is not seen, but in its place a portion of the basal hematodocha (*bh*) appears as the most basal part. The tegulum (*t*), embolus (*e*), and well-developed conductor (*c*) are all readily visible. The median apophysis (*ma*) is large and has a serrated ventral edge. In a dorsomesal view of an expanded right palpus (Fig. 23), the subtegulum (*st*) has been moved into view. The ectad rotation of the median apophysis (*ma*) has revealed a small hook on the dorsal surface. The embolus (*e*) and conductor (*c*) are fused for about two-thirds of their length. Other sclerites of the embolic subdivision seem to be absent, although the swollen base of the embolus possibly represents a reduced radix.

Araniella displicata (Hentz)
Figs. 24, 25

Chamberlin and Ivie (1942) removed this species from *Araneus* and made it the type species of their new genus *Araniella.* Unfortunately, they did not present figures of the type species.

I studied the palpus in detail. In an ectal view of an unexpanded right palpus (Fig. 24), the subtegulum (*st*) appears cupped, as if it has taken on the function of the conductor in this species. The very large tegulum (*t*) is easily visible. The basal part of the embolus (*e*) seems to be fused to the tegulum. The basal part of the median apophysis (*ma*) is hidden by the cymbium (*cy*). In an ectal view of an expanded right palpus (Fig. 25), the reduction of the subtegulum (*st*) characteristic of this family, as described by Archer (1951), is clearly seen. The basal part of the median apophysis (*ma*) is visible and there is a small "hematodocha" around the base of the embolus (*e*) and median apophysis. This area of lightly sclerotized tissue may represent a vestigial distal hematodocha, but due to the absence of any sclerites morphologically distal to the embolic subdivision, this "hematodocha" is best considered an articulating membrane between the tegulum (*t*) and the median apophysis.

Singa pratensis Emerton
Figs. 26, 27

The members of the genus *Singa* are structurally close to the theridiids (Kaston, 1948), but the structure of the palpus is closer to *Araneus* than are some species formerly considered to be in *Araneus*. According to Kaston (1948), who figures the palpus and epigynum, the species of *Singa* resemble one another so closely in form and appearance that they can be separated only by examining the external genitalia.

By comparing a mesal view of an unexpanded right palpus (Fig. 26) with the palp of *Araneus sericatus* (Fig. 19), one sees that the relative sizes of the structures correspond closely. The subtegulum (*st*) is reduced. The tegulum (*t*), median apophysis (*ma*), and terminal apophysis (*ta*) are all visible. The expanded right palpus in ectal view (Fig. 27) bears close resemblance to the expanded palpus of *Araneus sericatus* (Fig. 20). The sclerites of the embolic subdivision are all visible in essentially the same positions as in *Araneus sericatus,* but the radix of *Araneus sericatus* is in a slightly different position (Fig. 21).

Neoscona arabesca (Walckenaer)

The genus *Neoscona* is closely allied to *Araneus*. The males bear complex palpal organs built around the general *Araneus* plan. Expansion delineates the relationships of the various sclerites in much the same way as in *Araneus sericatus, Araneus nordmanni,* and *Singa pratensis*.

Mangora gibberosa (Hentz)
Figs. 28, 29

Mangora gibberosa has a complex palpus that, due to the displacement of the sclerites, seems even more complex than it really is. In an ectal view of an unexpanded right palpus (Fig. 28), the subtegulum (*st*) is visible and is large for a member of the family Araneidae. The tegulum (*t*) and terminal apophysis (*ta*) are separated by a large radix (*r*), the sheet-like, membranous conductor (*c*), and the enlarged base of the embolus (*e*). In a ventroectal view of an expanded right palpus (Fig. 29), the hematodochae seem to appear very much reduced, and most of the sclerites occupy positions different from those of the previously described araneids. In addition, the conductor is much enlarged.

Cyclosa conica (Pallas)

Kaston (1948) gave a figure of the palpus of the male of *Cyclosa conica.* In the degree of palpal complexity and reduction of hematodochae, this species lies somewhere between *Argiope trifasciata* and *Mangora gibberosa.* As in *Mangora,* the sclerites are much displaced, making them difficult to identify. Expansion causes an ectad rotation and further displacement, but, after treatment, individual sclerites can be seen as entities and at least tentatively identified. The median apophysis is bifurcate, as in many araneids, and the distal lobe is sigmoid. As in *Mangora,* the conductor is large and membranous and interferes with identification of the sclerites in the unexpanded palpus.

Family AGELENIDAE

The genitalia of some agelenids have been studied intensively with regard to their form and function (Gering, 1953). The palpus is moderately complicated, with a reduced subtegulum and a well-developed conductor that serves, at least in *Agelenopsis,* as a locking device during copulation (Gering, 1953).

Wadotes calcaratus (Keyserling)
Figs. 30, 31, 32

Muma (1947) revised the genus *Wadotes* and figured only individual sclerites rather than complete palpal organs. He considered the terminal apophysis to be of unusual value in taxonomic decisions.

In a ventral view of an unexpanded right palpus (Fig. 30), the subtegulum (*st*), tegulum (*t*), and embolus (*e*) are easily seen, as is the terminal apophysis (*ta*). In an ectal view of an expanded right palpus (Fig. 31), the distal portion of the embolus (*e*) is extensive and threadlike. Muma (1947) refers to the embolus as lying along a distinct conductor, but it seems to me that the only structure one can suggest as a conductor is solidly fused to the terminal apophysis. In a mesal view of an expanded right palpus (Fig. 32), the feature most noticeable is the distinctly annulated subtegulum (*st*).

Coras lamellosus (Keyserling)

Muma (1946) revised the North American members of the genus *Coras* and figured the palpi of a number of species, including *Coras lamellosus*. The palpus is very much like that of *Wadotes calcaratus* in the general arrangement of sclerites. After expansion, a general ectad rotation brings the long, thin embolus into full view. The conductor can be seen as separate from the terminal apophysis, and there is a twisted median apophysis that before expansion was concealed by the conductor and terminal apophysis.

Agelenopsis utahana (Chamberlin and Ivie)
Figs. 33, 34

This is one of the species used by Gering (1953) in a monumental study of the structure and function of the external genitalia of the genus *Agelenopsis,* and he gives several very useful figures of the expanded palpus.

In an ectal view of the unexpanded right palpus (Fig. 33), the embolus (*e*) is seen to be long, heavy, and spirally coiled. The tegulum (*t*) is somewhat indented to accommodate the embolus. In a mesal view of an expanded right palpus (Fig. 34), the fused basal and middle hematodochae (*bh-mh*) are visible. The subtegulum (*st*) has been pushed into view, and the conductor (*c*) has rotated mesad. Gering (1953) refers to the basal part of the embolus as the radix, and this may be morphologically correct.

Tegenaria domestica (Clerck)
Figs. 35, 36

Tegenaria domestica is a common house spider often referred to as *Tegenaria derhami* (Scopoli), and its habits have been studied extensively. The legs and palpal segments of this species are elongate.

In a ventral view of the unexpanded right palpus (Fig. 35), the cymbium (*cy*) bears a long distal finger. The tegulum (*t*), median apophysis (*ma*), and embolus (*e*) are fused into one sclerite capping the hematodochae. In an ectoventral view of an expanded right palpus (Fig. 36), the fused basal (*bh*) and middle hematodochae (*mh*) are inflated. The "cap" has been rotated ectad, and the hook-like conductor (*c*) has been extended on a short articulating membrane. No subtegulum was evident in this palpus, but an area on the basal hematodocha that is more heavily sclerotized than the rest of the hematodocha may correspond to the subtegulum.

Cicurina robusta Simon

Figs. 37, 38

Exline (1936) and Chamberlin and Ivie (1940) examined representatives of the genus *Cicurina,* and both gave excellent figures, concentrating on the tibia, which in males of this genus is uniquely developed. Frequently they neglected to provide figures of the palpal organ itself.

In an ectal view of an unexpanded left palpus (Fig. 37), the hooked conductor (*c*), the radix (*r*), and the embolus (*e*) are all visible, at least in part. The unusual tibial apophysis (*ti*) extends up the ectal side of the cymbium (*cy*). In an ectal view of an expanded right palpus (Fig. 38), the flattened subtegulum (*st*) has become visible, and the cupped tegulum (*t*) accommodates the radix (*r*) and the base of the embolus (*e*). The long and spirally wound embolus tapers to a hairlike tip. The hooked conductor (*c*) is extended.

Family LYCOSIDAE

This is a large and homogeneous family of which *Lycosa* is the principal genus. The palpi of most lycosids are similar to one another in general plan.

Lycosa ammophila Wallace

Wallace (1942) studied the *lenta* group of the genus *Lycosa* and described a number of new species, including *Lycosa ammophila,* from southeastern United States. Wallace gave figures of the palpus in ventral view, but emphasized the median apophysis, which he also figured separately in outline. In the unexpanded palpus, most of the features are readily visible. Expansion does, however, clarify relationship among the sclerites.

Family CLUBIONIDAE

The palpi of this family are simple, except for those of certain genera belonging to the subfamily Liocraninae and none of these are considered here. The palpal organs of most liocranines are similar to those of the Agelenidae.

Clubiona bryantae Gertsch
Figs. 39, 40

Gertsch (1941) proposed *Clubiona bryantae* as a new name for *Clubiona agrestis* Emerton, but he gave no figures. The new name was accepted by Edwards (1958), who gave several figures of the male palpus.

In an ectal view of an unexpanded right palpus (Fig. 39), the subtegulum (*st*), tegulum (*t*), and embolus (*e*) are subequal. The expanded right palpus (Fig. 40) shows the ectad rotation of the embolus (*e*), exposing its fingerlike tip.

Aysha gracilis (Hentz)
Figs. 41, 42

Aysha and a number of related genera (*Anyphaena, Anyphaenella, Gayenna,* and others) are often placed in a separate family, the Anyphaenidae, on which no recent work has been done.

In a ventral view of an unexpanded right palpus (Fig. 41), the tegulum (*t*) is large and extends below the alveolus or cavity of the cymbium (*cy*). The embolus (*e*) has a large, rotate, flattened base, and then tapers to a fine point, cupped by a projection of the cymbium. In a mesal view of an expanded right palpus (Fig. 42), all the parts appear to have been pushed ectad, and the subtegulum (*st*) is now visible. The track of the internal sperm duct through the tegulum is prominent.

Family SALTICIDAE

The Salticidae is considered by some authorities to contain the most advanced of spiders (Kaston, 1948), but the palpi are highly simplified.

Metacyrba undata (De Geer)
Figs. 43, 44

In a ventral view of an unexpanded right palpus of *Metacyrba undata* (Fig. 43), little is visible except the tegulum (*t*), which is enlarged and greatly extended proximally into a hollow on the

ventral surface of the palpal tibia (*ti*), and the fused embolus-conductor (*e, c*). In the ectodorsal view of an expanded palp (Fig. 44), the basal hematodocha (*bh*) is large and displaces all the sclerites ectad. The subtegulum (*st*) is visible as a small, sclerotic ring.

Tutelina elegans (Hentz)
Figs. 45, 46

Kaston (1952) gave figures showing the general appearance of this species, but he did not illustrate the genitalia. In a ventral view of an unexpanded right palpus (Fig. 45), the general appearance is essentially the same as in *Metacyrba undata*, but no recognizable conductor is present on or near the embolus (*e*). Expansion of the palpus (Fig. 46) brings about an ectad rotation and, in an ectodorsal view, the subtegulum (*st*) is exposed.

Salticus scenicus (Clerck)

This species is distributed throughout the United States and Europe and has been widely studied. The palpus is very simple and follows the general plan of the two previously described species of the family Salticidae. In the expanded palpus, the basal hematodocha is greatly expanded, and the subtegulum is brought into view.

Family ULOBORIDAE

This family was recently revised by Muma and Gertsch (1964), and a number of new species were described. Figures were given of unexpanded palpi and individual segments, but an error was made in the figure titles.

The palpi of these spiders are remarkable for the extreme development of certain sclerites. The habits of the Uloboridae are unique, but among some species the modes of web-building converge with those of the Araneidae. This behavioral convergence is not reflected in the morphology of the palpal organs of the males.

Hyptiotes cavatus Hentz
Figs. 47, 48, 49

Muma and Gertsch (1964) illustrate the entire palpus of *Hyptiotes cavatus* and also give a figure of what they call the "tip of the embolus." Close examination of actual specimens and of the textual description given by Muma and Gertsch leaves little doubt

that this figure actually represents the tip of the median apophysis.

In an ectal view of an unexpanded right palpus (Fig. 47), the most striking feature is the large, elongated median apophysis (*ma*) with its membranous tip. The tegulum (*t*) and subtegulum (*st*) are almost completely covered by the enlarged membranous conductor (*c*). The embolus (*e*) originates mesally and coils around the other sclerites of the palpal organ. In a mesal view of the same palpus (Fig. 48), the origin of the embolus (*e*), as well as its attenuated distal part entering the conductor (*c*), is easily seen. The conductor is accompanied by the long, hooked radix (*r*). An ectoventral view of an expanded right palpus (Fig. 49) shows that expansion has resulted in little change, but the whole of the distal part of the embolus (*e*) can now be seen and its relationship to the median apophysis (*ma*) is clear.

Family DICTYNIDAE

Chamberlin and Gertsch (1958) revised this family, of which *Dictyna* is the largest genus. While the palpal organs of all North American species of *Dictyna* are similar, Chamberlin and Gertsch separated species on the basis of the structure of the tip of the embolus.

Dictyna sublata (Hentz)

Figs. 50, 51

In a mesal view of an unexpanded right palpus (Fig. 50) of *Dictyna sublata,* the embolus (*e*) appears heavy and coiled and distally enters the large shieldlike conductor (*c*). The path of the sperm tube can be traced through the tegulum (*t*) and the base of the embolus. A ventral view of an expanded right palpus (Fig. 51) shows that an almost complete ectad rotation of the base of the embolus has occurred. The subtegulum (*st*), as well as the basal and middle hematodochae (*bh, mh*), is visible.

DISCUSSION

For purposes of discussion, the males of species used in this study can be separated into three groups: those with very complex palpi, those with moderately complex palpi, and those with simple palpi.

Drapetisca alteranda, Linyphia marginata, Araneus sericatus, Araneus nordmanni, Neoscona arabesca, Cyclosa conica, Singa pratensis, Mangora gibberosa, and *Hyptiotes cavatus* fall in the

group having very complex palpi. In this group almost all possible sclerites are present in a more or less highly developed form. These species are especially characterized by the number of sclerites distal to the embolus. Males of species of *Drapetisca* and *Linyphia* have palpi in which the lateral subterminal apophysis is developed into a large shield covering the whole organ. In species of *Araneus* and *Singa*, the male palpus has many structures concealed by other sclerites and by the manner in which the palpus is folded. In males of *Mangora*, *Cyclosa*, and *Hyptiotes* displacement of the sclerites has caused confusion when unexpanded palpi are used in the description of species. Expanding the palpus can be of great value in this group.

In the group with moderately complex male palpi are: *Enoplognatha tecta, Theridion differens, Theridion frondeum, Steatoda borealis, Argiope trifasciata, Araniella displicata, Wadotes calcaratus, Agelenopsis utahana, Coras lamellosus, Cicurina robusta, Lycosa ammophila,* and *Dictyna sublata.* This group is characterized by the approximately equal development of most sclerites. The apical division is poorly represented, and some of the sclerites of the embolic subdivision are reduced. Usually the basal hematodocha is well developed. When the palpus is moderately complex, one has to use his own judgment whether or not expansion will be worthwhile. The process of expansion has the value of making relationships clear and exposing portions of sclerites that may be hidden, because in most species in this group the full complement of sclerites (except the subtegulum) is usually visible before expansion.

The third group, species with simple male palpi, includes: *Soulgas corticarius, Ceratinopsidis formosa, Tegenaria domestica, Clubiona bryantae, Aysha gracilis, Metacyrba undata, Salticus scenicus,* and *Tutelina elegans.* These spiders have palpi characterized by the loss, fusion, or reduction of sclerites. Expansion seems to be of little utility in this group.

The process of expansion seems to have its greatest value in studying species with complex palpi. The complex palpus may indicate specialization and occurs in three very highly specialized families (Theridiidae, Linyphiidae, Araneidae). However, spiders of a fourth very specialized family, the Salticidae, have a simple type of palpus.

If the hematodochae of a complex palpus are reduced, expansion does not show structures that were not visible in the unexpanded palpus. In such cases, a delicate dissection of the palpus

may be indicated. The need for expansion may also be partly obviated by the presence of other taxonomically useful sexual modifications, such as the ornate third leg of some salticid males or the tibial apophyses and cephalic modifications of the micryphantids.

SUMMARY

1. Several methods have been suggested for expanding the palpi of male spiders for taxonomic purposes. The method used in this study involved immersing the palpus for 6-8 hours in a 10 per cent KOH solution, followed by a quick transfer to distilled water. Expanded palpi were stored in 70 per cent ethanol solution.
2. The expanded palpus of each of 29 species of spiders was compared with the unexpanded palpus of the same species to determine if any parts not observable in the unexpanded palpus could be seen in the expanded palpus.
3. The process of expansion was found to be most useful in species with complex palpi and least useful in species with simple palpi.
4. Under certain conditions, such as the reduction of hematodochae, many features of complex palpi were still obscure.
5. The experimenter must use his own judgment in deciding when the process of expansion is worthwhile, but certainly more detailed examination of palpi after expansion can be of benefit in the present confused state of spider taxonomy.

LITERATURE CITED

Alexander, A. J., and D. W. Ewer.
1957. On the origin of mating behavior in spiders. Amer. Natur. **91**: 311-317.

Archer, A. F.
1951. Studies in the orbweaving spiders (Argiopidae). 1. Amer. Mus. Novit. No. **1487**: 1-52.

Barrows, W. M.
1925. Modification and development of the arachnid palpal claw, with especial reference to spiders. Ann. Entomol. Soc. Amer. **18**: 483-516.

Bishop, S. C., and C. R. Crosby.
1930. Studies in American spiders: genera *Ceratinopsis, Ceratinopsidis,* and *Tutaibo*. J. New York Entomol. Soc. **38**: 15-34.

Blauvelt, H. H.
1936. The comparative morphology of the secondary sexual organs of *Linyphia*. Festschr. Embrik Strand **2**: 81-171.

CHAMBERLIN, R. V., and W. J. GERTSCH
1958. The spider family Dictynidae in America north of Mexico. Bull. Amer. Mus. Natur. Hist. **116**: 1-152.
CHAMBERLIN, R. V., and W. IVIE
1940. Agelenid spiders of the genus *Cicurina*. Bull. Univ. Utah, Biol. Ser. **5**(9): 1-108.
1942. A hundred new species of American spiders. Bull. Univ. Utah, Biol. Ser. **7**(1): 1-117.
1943. New genera and species of North American linyphiid spiders. Bull. Univ. Utah, Biol. Ser. **7**(6): 1-39.
COMSTOCK, J. H.
1940. The spider book, revised and edited by W. J. Gertsch. Comstock Publishing Company, New York. 721 pp.
CROSBY, C. R., and S. C. BISHOP
1936. Studies in American spiders: miscellaneous genera of Erigoneae. Festschr. Embrik Strand **2**: 52-64.
EDWARDS, R. J.
1958. The spider subfamily Clubioninae of the United States, Canada and Alaska (Araneae: Clubionidae). Bull. Mus. Comp. Zool. **118**: 365-436.
ENGELHARDT, V.
1910. Beiträge zur Kenntnis der weiblichen Copulationsorgane einiger Spinnen. Z. Wiss. Zool. **96**: 32-117.
EXLINE, H.
1936. Nearctic spiders of the genus *Cicurina* Menge. Amer. Mus. Novit. No. **850**: 1-26.
GERING, R. L.
1953. Structure and function of the genitalia in some American agelenid spiders. Smithson. Misc. Collec. **121**(4): 1-84.
GERTSCH, W. J.
1941. New American spiders of the family Clubionidae. II. Amer. Mus. Novit. No. **1148**: 1-18.
1949. American spiders. D. Van Nostrand Publishing Company, Inc., New York. 285 pp.
1951. New American linyphiid spiders. Amer. Mus. Novit. No. **1514**: 1-11.
GERTSCH, W. J., and I. DAVIS
1946. Report on a collection of spiders from Mexico. V. Amer. Mus. Novit. No. **1313**: 1-11.
KASTON, B. J.
1948. Spiders of Connecticut. Connecticut State Geol. Natur. Hist. Surv. Bull. **70**: 1-874.

KASTON, B. J.
1952. How to know the spiders. Wm. C. Brown Company, Dubuque, Iowa. 220 pp.

LEVI, H. W.
1957a. The spider genera *Crustulina* and *Steatoda* in North America, Central America, and the West Indies (Araneae, Theridiidae). Bull. Mus. Comp. Zool. **117**: 367-424.
1957b. The spider genera *Enoplognatha, Theridion,* and *Paidisca* in America north of Mexico (Araneae, Theridiidae). Bull. Amer. Mus. Natur. Hist. **112**: 1-123.
1961. Evolutionary trends in the development of palpal sclerites in the spider family Theridiidae. J. Morphol. **108**: 1-9.
1965. Techniques for the study of spider genitalia. Psyche **72**(2): 152-158.

MERRETT, P.
1963. The palpus of male spiders of the family Linyphiidae. Proc. Zool. Soc. London **140**(3): 347-467.

MUMA, M.
1946. North American Agelenidae of the genus *Coras* Simon. Amer. Mus. Novit. No. **1329**: 1-20.
1947. North American Agelenidae of the genus *Wadotes* Chamberlin. Amer. Mus. Novit. No. **1334**: 1-12.

MUMA, M., and W. J. GERTSCH.
1964. The spider family Uloboridae in North America north of Mexico. Amer. Mus. Novit. No. **2196**: 1-43.

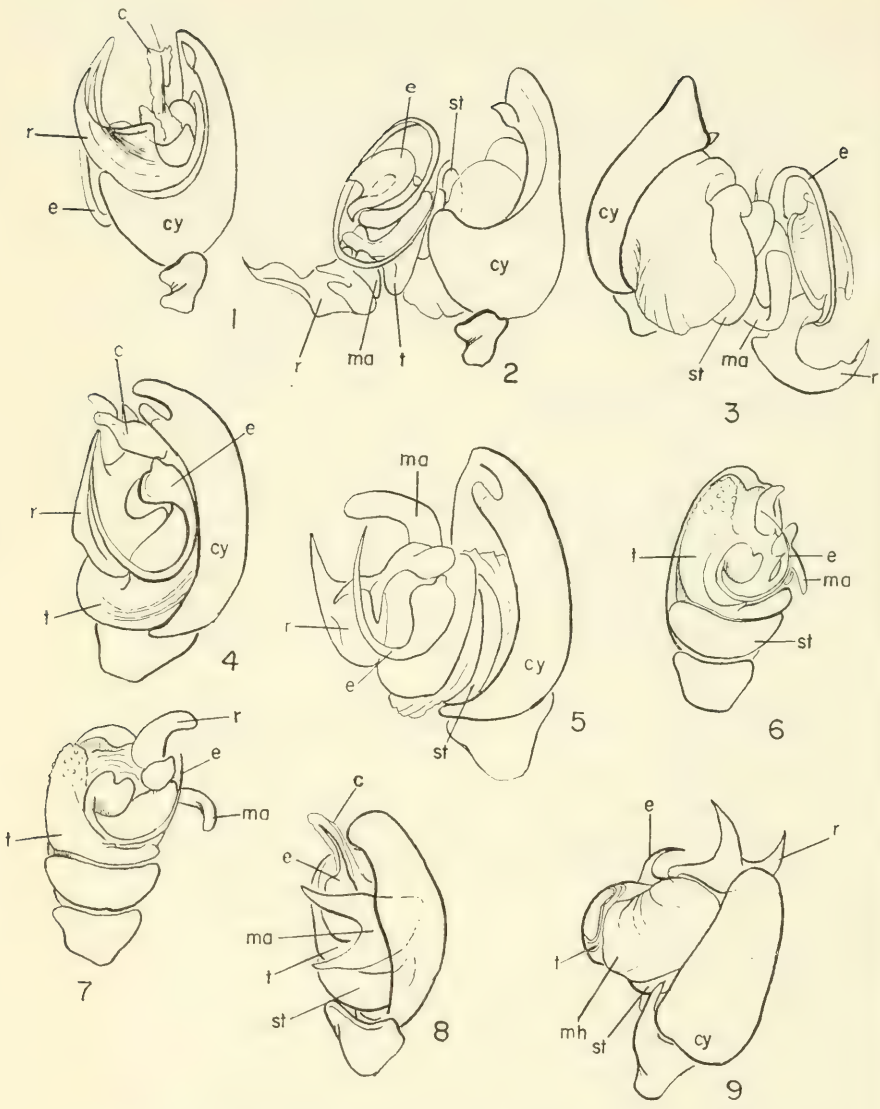
PETRUNKEVITCH, A.
1925. External reproductive organs of the common grass spider, *Agelena naevia* Walckenaer. J. Morphol. **40**: 559-573.

SAVORY, T. H.
1928. The biology of spiders. Sidgwick and Jackson, London. 376 pp.

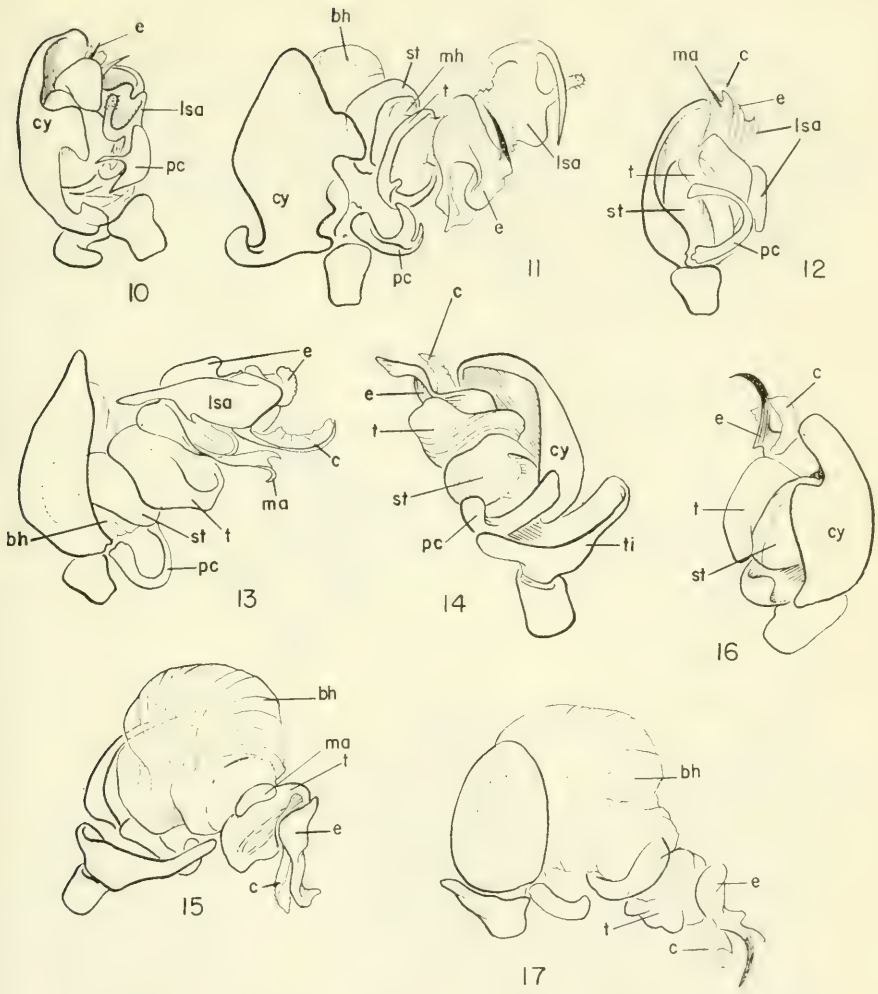
WALLACE, H. K.
1942. A study of the *lenta* group of the genus *Lycosa* with descriptions of new species (Araneae, Lycosidae). Amer. Mus. Novit. No. **1185**: 1-21.

ABBREVIATIONS USED IN FIGURES

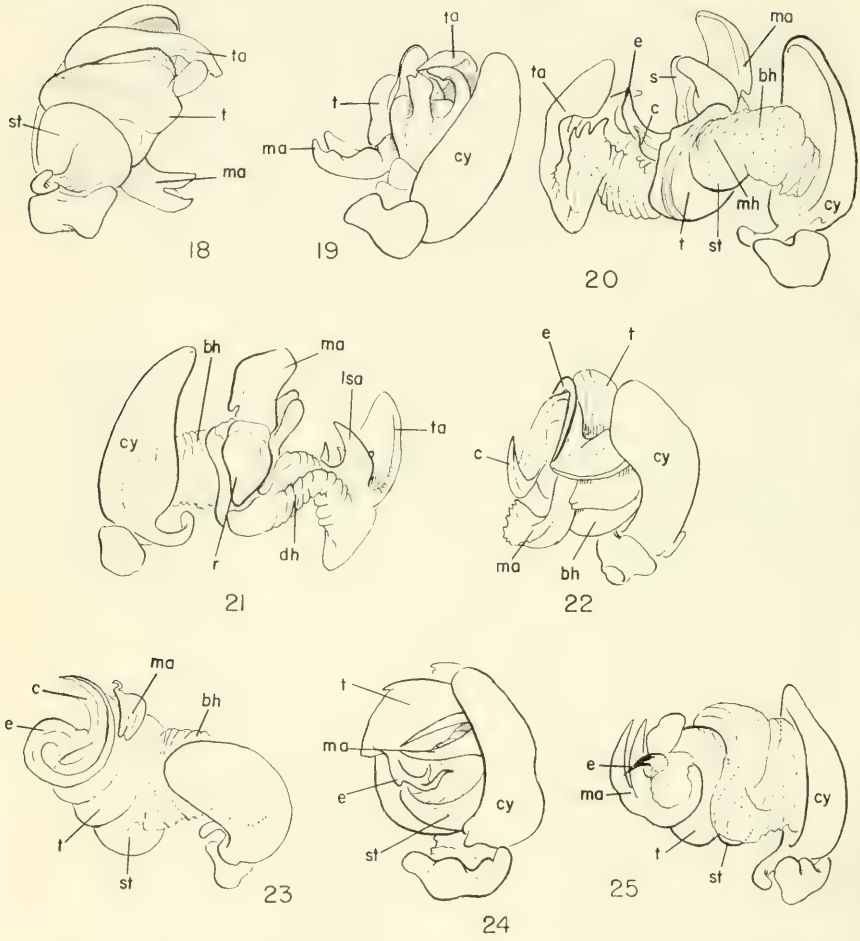
bh	basal hematodocha
c	conductor
cy	cymbium
dh	distal hematodocha
e	embolus
lsa	lateral subterminal apophysis
ma	median apophysis
mh	middle hematodocha
pc	paracymbium
r	radix
s	stipes
st	subtegulum
t	tegulum
ta	terminal apophysis
ti	tibia



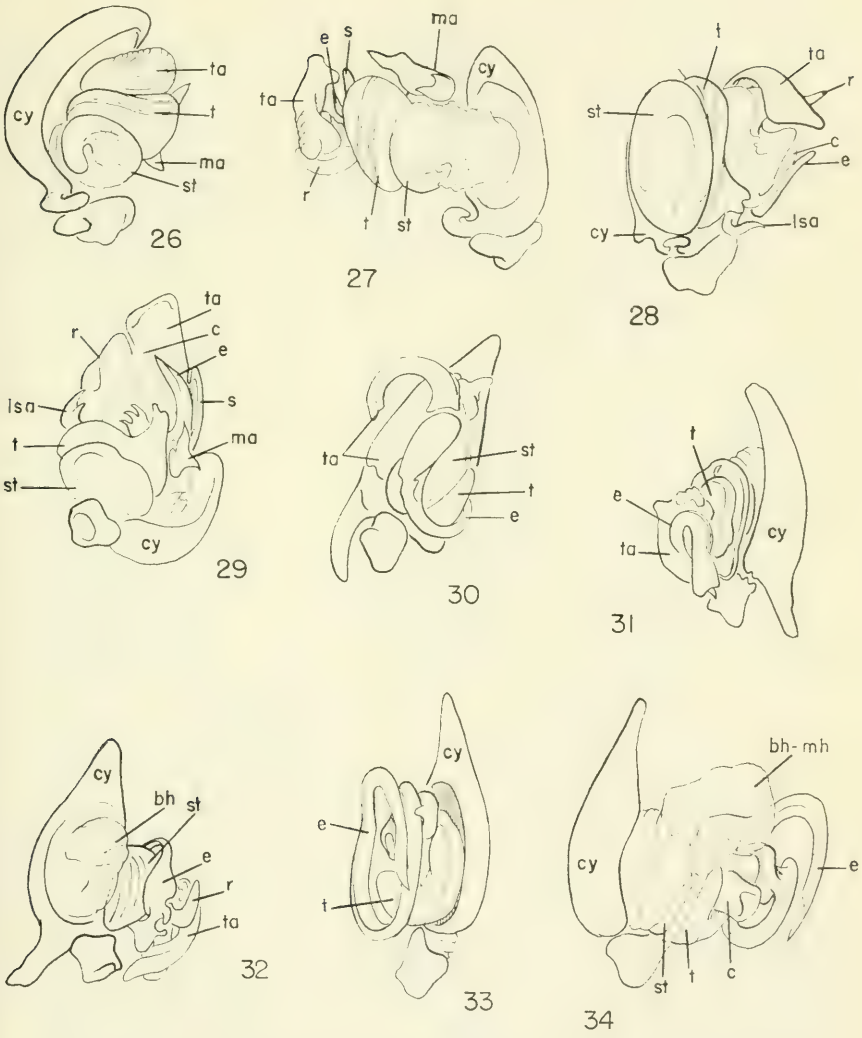
FIGS. 1-3. *Steatoda borealis*. 1, Mesal view of an unexpanded right palpus. 2, Mesal view of an expanded right palpus. 3, Ectal view of an expanded right palpus. FIGS. 4, 5. *Enoplognatha tecta*. 4, Ectal view of an unexpanded left palpus. 5, Ectal view of an expanded left palpus. FIGS. 6, 7. *Theridion differens*. 6, Ventral view of an unexpanded right palpus. 7, Ventral view of an expanded right palpus. FIGS. 8, 9. *Theridion frondeum*. 8, Ventral view of an unexpanded right palpus. 9, Ventral view of an expanded right palpus.



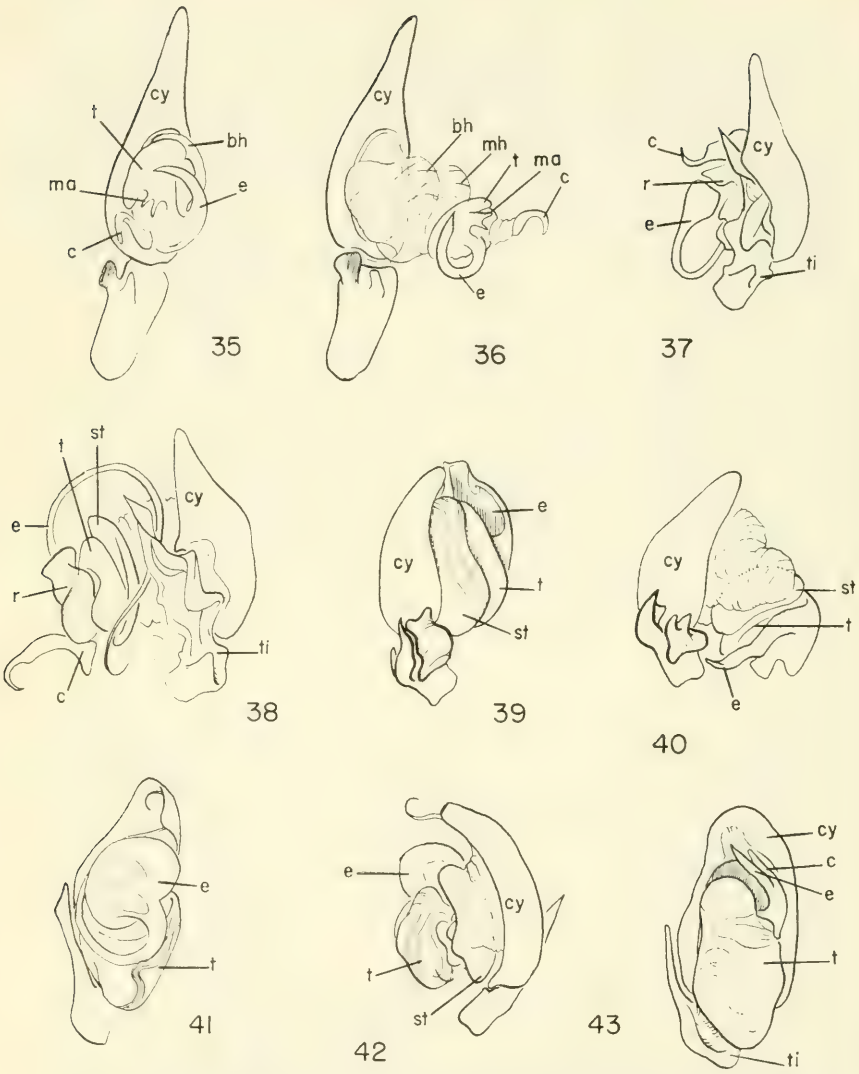
FIGS. 10, 11. *Drapetisca alteranda.* 10, Mesal view of an unexpanded right palpus. 11, Mesal view of an expanded right palpus. FIGS. 12, 13. *Linyphia marginata.* 12, Ectal view of an unexpanded right palpus. 13, Ectal view of an expanded right palpus. FIGS. 14, 15. *Soulgas corticarius.* 14, Ectal view of an unexpanded right palpus. 15, Mesal view of an expanded right palpus. FIGS. 16, 17. *Ceratinopsidis formosa.* 16, Ectal view of an unexpanded right palpus. 17, Dorsoectal view of an expanded right palpus.



FIGS. 18-21. *Araneus sericatus*. 18, Ventral view of an unexpanded right palpus. 19, Mesal view of an unexpanded right palpus. 20, Ectal view of an expanded right palpus. 21, Mesal view of an expanded right palpus. FIGS. 22, 23. *Argiope trifasciata*. 22, Mesal view of an unexpanded right palpus. 23, Dorsomesal view of an expanded right palpus. FIGS. 24, 25. *Araniella displicata*. 24, Ectal view of an unexpanded right palpus. 25, Ectal view of an expanded right palpus.



FIGS. 26, 27. *Singa pratensis*. 26, Mesal view of an unexpanded right palpus. 27, Ectal view of an expanded right palpus. FIGS. 28, 29. *Mangora gibberosa*. 28, Ectal view of an unexpanded right palpus. 29, Ventroectal view of an expanded right palpus. FIGS. 30-32. *Wadotes calcaratus*. 30. Ventral view of an unexpanded right palpus. 31, Ectal view of an expanded right palpus. 32, Mesal view of an expanded right palpus. FIGS. 33, 34. *Agelenopsis utahana*. 33, Ectal view of an unexpanded right palpus. 34, Mesal view of an expanded right palpus.



Figs. 35, 36. *Tegenaria domestica.* 35, Ventral view of an unexpanded right palpus. 36, Ectoventral view of an expanded right palpus. Figs. 37, 38. *Cicurina robusta.* 37, Ectal view of an unexpanded right palpus. 38, Ectal view of an expanded right palpus. Figs. 39, 40. *Clubiona bryantae.* 39, Ectal view of an unexpanded right palpus. 40, Ectal view of an expanded right palpus. Figs. 41, 42. *Aysha gracilis.* 41, Ventral view of an expanded right palpus. 42, Mesal view of an unexpanded right palpus. Fig. 43. *Metacyrba undata,* ventral view of an unexpanded right palpus.

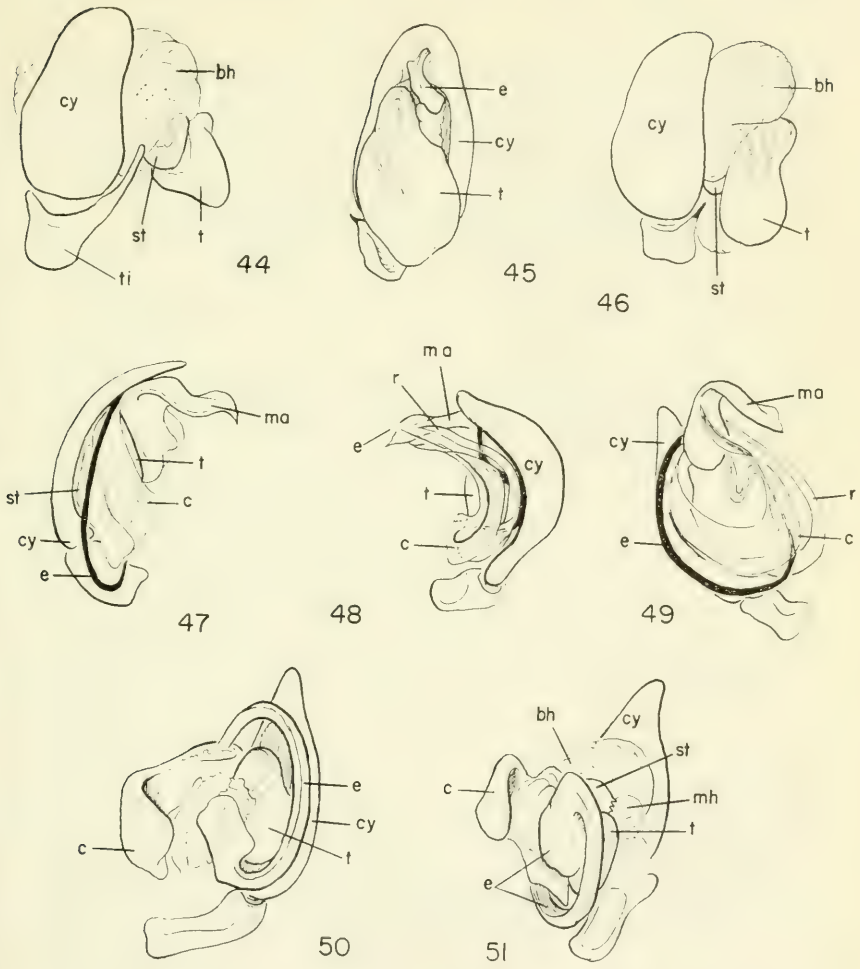


FIG. 44. *Metacyrba undata,* ectodorsal view of an expanded right palpus. FIGS. 45, 46. *Tutelina elegans.* 45, Ventral view of an unexpanded right palpus. 46, Ectodorsal view of an expanded right palpus. FIGS. 47-49. *Hyptiotes cavatus.* 47, Ectal view of an unexpanded right palpus. 48, Mesal view of an unexpanded right palpus. 49, Ectoventral view of an expanded right palpus. FIGS. 50, 51. *Dictyna sublata.* 50, Mesal view of an unexpanded right palpus. 51, Ventral view of an expanded right palpus.

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Museum of Comparative Zoology

CAMBRIDGE, MASS. 3 FEBRUARY, 1967 NUMBER 260

MONOGRAPH OF THE GENUS *SPIROCERAMUS* (MOLLUSCA: PULMONATA: UROCOPTIDAE)

By William J. Clench

The last complete monograph of the family Urocoptidae was that of H. A. Pilsbry, 1902-1904, in the second series of the Manual of Conchology. At that time only a single species was credited to the genus *Spiroceramus*. This species was *S. amplus* (Pfeiffer) from the region of Bayamo in the south of Oriente Province in eastern Cuba. Since then, C. G. Aguayo has described a species from the northern portion of Oriente Province, and I have described two species from the Bahamas, one from Little Abaco in the northern part, and one from Acklin's Island in the southern part of the Bahamian Archipelago. Two new species are described in this report from the Sierra de Cubitas, an isolated mountain system in north-central Camagüey Province in central Cuba.

With comparatively few exceptions the West Indian Urocoptidae are strictly calciphiles, living on limestone rocks where they feed on the encrusting lichens. A very few are arboreal. The Bahamian species were living on or under stones; the Cuban species on the limestone ledges. Under optimum conditions they can exist in incredible numbers, usually preferring shade, but they also exist on the limestone with no shade at all. They are active at night and during periods of rain.

UROCOPTIDAE

Genus SPIROCERAMUS Pilsbry and Vanatta

Spiroceramus Pilsbry and Vanatta, 1898, Proc. Acad. Nat. Sci. Philadelphia, **50**: 281 (type species, *Macroceramus amplus* Pfeiffer, original designation).

Shells thin, cylindrical, and composed of many narrow whorls. Spire acute, the apex entire, not deciduous. Colored a pale brownish with patches of white. Sculptured with fine oblique striae.

Whorls 9 to 15, convex, early whorls straight or slightly angular. Aperture somewhat oblique, subcircular, and the lip narrowly reflected. Suture indented, smooth or crenulate. Axis twisted or encircled with a thin spiral lamella.

Pilsbry (1904, p. 172), on the basis of the then known single species *S. amplus*, stated that it had the shape of *Holospira*, the axis of *Arangia*, and the aperture and protoconch of *Microceramus*. This statement can still stand with only the slight modification that all species do not have a spiral lamella on the axis and certain species possess a crenulated suture.

Subgenus Spiroceramus Pilsbry and Vanatta

Species with or without the spiral lamella on the axis and having the oblique sculpture of fine striae similar on all whorls. The suture with or without crenulations.

Spiroceramus (Spiroceramus) amplus (Pfeiffer)

Plate 1, figures 6, 7

Macroceramus amplus Gundlach, 1856, [*in*] F. Poey, Memorias Sobre la Historia Natural de la Isla de Cuba, Habana **2:** 8, no. 378 (Cuba). [*Nomen nudum.*]

Macroceramus amplus 'Gundlach' Pfeiffer, 1858, Malakozoologische Blätter **5:** 44 (Guisa [Bayamo, Oriente], Cuba); Pfeiffer, 1859, Monographia Heliceorum Viventium **4:** 689; Pfeiffer, 1868, Novitates Conchologicae **3:** 383, pl. 89, figs. 12-14; Arango, 1878, Contribucion a la Fauna Malacologica Cubana, Habana, p. 84 (Guisa and San Andres, Bayamo, Cuba). [Syntypes, MCZ 39318.]

Microceramus (*Spiroceramus*) *amplus* Pfeiffer. Pilsbry, 1904, Man. of Conch. (2) **16:** 172, pl. 26, figs. 24, 29.

Measurements

Height mm	Width mm	
10.5	3.9	Syntype. Guisa, Bayamo, Cuba
11.1	4.	Syntype. Guisa, Bayamo, Cuba
11.1	3.3	Syntype. Sao Arriba, Holguin, Cuba

Description: Shell reaching 11.1 mm in height, minutely umbilicate, cylindrical, attenuate, the upper third rapidly tapering to the early whorls and sculptured. Whorls 14 to 15, convex, those on the upper one-third slightly angled. Color a light grayish brown and mottled with a dull white. Spire extended, the lower two-thirds nearly parallel sided, the conic one-third forming an

angle of about 35°. Aperture subcircular, with the outer lip slightly reflected. Inner or parietal lip reflexed over the minute umbilicus. Axis twisted and forming a broad lamella. Columella short and slightly angled. Suture deeply impressed. Sculpture consisting of numerous and fine, oblique striae. Protoconch with 1½ whorls and sculptured with fine, oblique striae.

Remarks: This is rather a remarkable species for any member of the Urocoptidae as it occurs in two distinct and well separated areas. Holguin is about 70 kilometers NE of Bayamo with much relatively flat country between them.

Specimens examined: CUBA. *Oriente Prov.:* Guisa, Bayamo; Cerro Moncada and Cerro San Juan, Sao Arriba, both Holguin.

SPIROCERAMUS (SPIROCERAMUS) BARBOURI Aguayo

Plate 1, figure 5

Spiroceramus amplus barbouri Aguayo, 1935, Mem. Soc. Cubana Hist. Nat., **9**: 126, pl. 9, figs. 3-4 (Paradones junto a la Curva de la Campana, Gibara [Oriente], Cuba). [Holotype, MCZ 237877. Additional paratypes from the same locality, MCZ 110570.]

Measurements

Height mm	Width mm	
5.5	2	Holotype
4.5	1.8	Paratype
4.75	2	Paratype
5.8	2	Paratype

Description: Shell reaching 5.8 mm in height, imperforate, cylindrical, attenuate, the upper third rapidly tapering to the early whorls and sculptured. Colored a light brown with most of the oblique costae and crenulations white. Whorls 9 to 11 and convex, the early 5 whorls straight-sided and vertical. Spire extended, the lower two-thirds nearly parallel sided, the conic one-third forming an angle of about 40°. Aperture subcircular, the outer lip simple and but slightly reflected. Axis twisted and forming a narrow lamella. Columella short and slightly angled. Suture impressed. Sculpture consisting of numerous and fine, oblique striae, many of which terminate above with crenulations at the suture. Protoconch with 1½ whorls and sculptured with fine and straight striae.

Remarks: Originally described as a subspecies of *S. amplus*, this present entity is a distinct species. *S. barbouri* is only one-half

the height of *amplus* and has a crenulated suture which *amplus* does not have, and the axial lamella is much narrower. So far as now known, this species is limited to the type locality.

Specimens examined: Holotype and paratypes.

Spiroceramus (Spiroceramus) pilsbryi new species

Plate 1, figure 3

Holotype: MCZ 188845, from Cerro de Tuabagüey, Sierra de Cubitas, Camagüey Province, Cuba.

Paratypes: MCZ 256082, from the type locality, and MCZ 188847 from Cueva del Circulo, Sierra de Cubitas, Camagüey Province, Cuba.

Measurements

Height mm	Width mm	
15.1	4.8	Holotype
13	4.1	Paratype MCZ 188847

Description: Shell reaching 15 mm in height, minutely umbilicate, tapering from the ninth whorl to the protoconch and sculptured. Whorls 13 to 14 and slightly convex. Color a light horn with numerous, irregular patches of white. Spire extended and forming an angle of about 36°. Aperture subcircular, the outer lip slightly reflexed and the inner or parietal lip reflected over the minute umbilicus. Axis twisted and forming a broad lamella. Columella angled and somewhat broadened. Suture indented and coarsely crenulated. Sculpture consisting of exceedingly fine, oblique striae. Protoconch with two very finely lirate whorls.

Remarks: S. pilsbryi and *S. vanattai,* both from the Sierra de Cubitas are very different from one another. *S. pilsbryi* differs from *vanattai* by being much larger, having the broad axial lamella, coarse sutural crenulations and very much finer sculpture. The conic taper toward the protoconch starts from near the center (ninth whorl) in *pilsbryi,* while in *vanattai* the entire shell from the body whorl tapers toward the protoconch.

This must represent quite a rare species, as only a very few specimens are known.

Specimens examined: Holotype and paratype.

SPIROCERAMUS (SPIROCERAMUS) VANATTAI new species

Plate 1, figure 4

Holotype: MCZ 256083, from Los Cangilones, Sierra de Cubitas, Camagüey Province, Cuba.

Paratypes: From the same locality (MCZ 131387; MCZ 80765), and from El Cercado de Cubitas, near Cueva del Circuto (MCZ 131388; MCZ 188846); Finca Santa Gertrudis, Minas (MCZ 80766); Corrales de Cangilones (MCZ 131390); Paso de los Burros (MCZ 131386); Paso Paredones (MCZ 131391); El Tuabagüey, near the Cueva del Indio (MCZ 188844), all Sierra de Cubitas, Camagüey Province, Cuba.

Measurements [1]

Height mm	Width mm	
9.4	4.6	Holotype
10	4.5	Paratype
8.6	4.5	Paratype
9	4.2	Paratype

Description: Shell reaching 10 mm in height, minutely umbilicate, conic, tapering from the body whorl to the protoconch and sculptured. Whorls 10 to 11 and moderately convex. Color light horn with irregular patches of white which cover mainly the oblique striae. Spire extended and forming an angle of 30°. Aperture subcircular, the outer lip slightly reflexed. Inner or parietal lip reflected over the minute umbilicus. Axis twisted but lacking a lamella. Columella short and slightly angled. Suture moderately indented and finely crenulate. Sculpture consisting of numerous and prominent oblique striae. Protoconch with 2 whorls and smooth.

Remarks: See Remarks under *S. pilsbryi*. Named for E. G. Vanatta who had been associated with H. A. Pilsbry at the Academy of Natural Sciences, Philadelphia.

Specimens examined: Holotype and paratypes.

Subgenus INSULACERAMUS new subgenus

Species with the axis twisted but not encircled with a spiral lamella. Early non-protoconch whorls rather coarsely lirate, later

[1] All specimens measured are from the type locality.

whorls finely lirate. Suture noncrenulate.

So far this subgenus is limited to the Bahama Islands. Specimens are exceedingly rare, as only three are known to represent the two species.

Type species: Microceramus (*Spiroceramus*) *greenwayi* Clench.

Spiroceramus (Insulaceramus) robertsoni (Clench)

Plate 1, figure 2

Microceramus (*Spiroceramus*) *robertsoni* Clench, 1963, Bull. Mus. Comp. Zool. **128:** 406, pl. 3, fig. 1 (Delectable Bay Settlement, Acklins Island, Bahama Islands). [Holotype, MCZ 225313.]

Measurements

Height mm	Width mm	
6.7	1.0	Holotype

Description: Shell reaching 6.7 mm in height, thin, imperforate, dull and sculptured. Color probably gray, whorls 11 and convex. First 5 to 6 whorls forming the conic portion of the spire. Aperture subcircular. Lip simple. Columella nearly straight. Axis simple and not twisted. Suture indented. Sculpture consisting of numerous, fine, oblique axial riblets. These riblets are somewhat stronger on the first 5 to 6 whorls.

Remarks: This species is closely related to *S. greenwayi* Clench from Fox Town, Little Abaco Island, Bahamas. It differs by being a little more coarsely sculptured and having the protoconch a little smaller.

Spiroceramus (Insulaceramus) greenwayi (Clench)

Plate 1, figure 1

Microceramus (*Spiroceramus*) *greenwayi* Clench, 1938, Mem. Soc. Cubana Hist. Nat., **12:** 329, pl. 25, fig. 1 (Fox Town, Little Abaco Island, Bahama Islands). [Holotype, MCZ 116688.]

Measurements

Height mm	Width mm	
6.5	1.9	Holotype

Description: Shell thin, small and imperforate. Color a dull isabelline (true color, however, cannot be given as the single

specimen was found dead). Whorls 11, early 6 whorls which form the cone strongly convex; later whorls much less so. Aperture subcircular, lip simple and slightly flaring. Columella concavely arched, not distinct but forming the inner margin of the aperture. Axis simple with only a very slight twist. Sculpture: nuclear whorl faintly costate; next five strongly costate with oblique somewhat sinuous riblets, generally whitish; remaining whorls finely costate. Suture deeply indented but not crenulate. Aperture cast at an angle of 40° from a base line.

Remarks: See under *S. robertsoni* (Clench).

Specimens examined: Holotype.

REFERENCES

Arango, Rafael
1878. Contribucion a la Fauna Malacologica Cubana, Habana, pp. 1-315.

Pilsbry, H. A.
1904. Manual of Conchology. (2) **16:** 1-329.

(Received 2 August, 1966.)

Plate 1

Fig. 1. *Spiroceramus* (*Insulaceramus*) *greenwayi* (Clench), Fox Town, Little Abaco Island, Bahama Islands (18.4 X). Holotype, MCZ 116688.

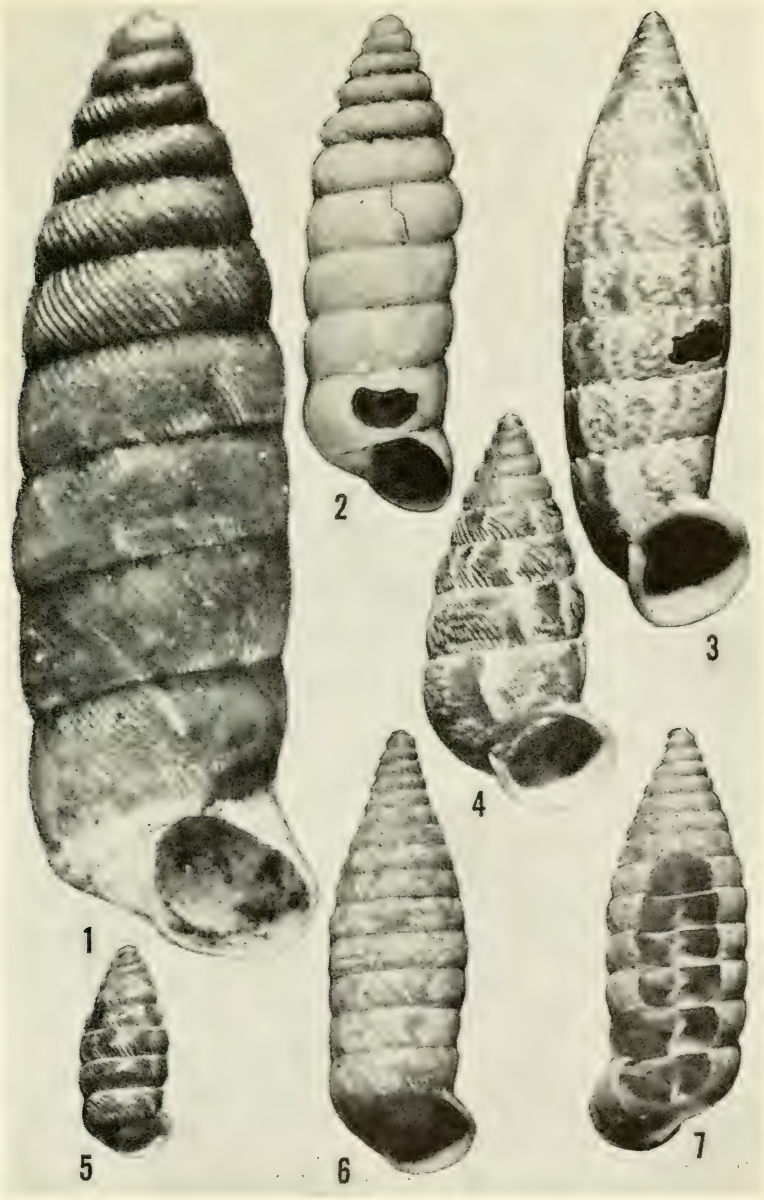
Fig. 2. *Spiroceramus* (*Insulaceramus*) *robertsoni* (Clench), Delectable Bay, Acklins Island, Bahama Islands (10 X). Holotype, MCZ 225313.

Fig. 3. *Spiroceramus* (*Spiroceramus*) *pilsbryi* n. sp., Cerro de Tuabagüey, Sierra de Cubitas, Camagüey, Cuba (5.3 X). Holotype, MCZ 188845.

Fig. 4. *Spiroceramus* (*Spiroceramus*) *vanattai* n. sp., Los Cangilones, Sierra de Cubitas, Camagüey, Cuba (5.3 X). Holotype, MCZ 256083.

Fig. 5. *Spiroceramus* (*Spiroceramus*) *barbouri* Aguayo, Curva de la Compana, Gibara, Oriente, Cuba (5.3 X). Holotype, MCZ 237877.

Figs. 6-7. *Spiroceramus* (*Spiroceramus*) *amplus* (Pfeiffer), Guisa, Bayamo, Oriente, Cuba (5.3 X). Syntypes, MCZ 39318. Figure 7 shows the axis and the spiral lamella.


1
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3
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6
7

Plate 2

Map showing distribution of the species. 1. *Spiroceramus* (*Spiroceramus*) *amplus* (Pfeiffer), Guisa, Bayamo, and Sao Arriba, Holguin, both Oriente, Cuba. 2. *Spiroceramus* (*Spiroceramus*) *barbouri* Aguayo, near Curva de la Campana, Gibara, Oriente, Cuba. 3. *Spiroceramus* (*Spiroceramus*) *pilsbryi* n. sp., Cerro de Tuabagüey, Sierra de Cubitas, Camagüey, Cuba. 4. *Spiroceramus* (*Spiroceramus*) *vanattai* n. sp., Los Cangilones, Sierra de Cubitas, Camagüey, Cuba. 5. *Spiroceramus* (*Insulaceramus*) *robertsoni* (Clench), Delectable Bay, Acklins Island, Bahama Islands. 6. *Spiroceramus* (*Insulaceramus*) *greenwayi* (Clench), Fox Town, Little Abaco Island, Bahama Islands.

BREVIORA

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THE *MONTICOLA* GROUP OF THE LIZARD GENUS *ANOLIS* IN HISPANIOLA

By

Richard Thomas and Albert Schwartz[1]

In 1962, Williams summarized the then available data on three allied species of Hispaniolan anoles: *A. monticola* Shreve, *A. christophei* Williams and *A. etheridgei* Williams (= *A. darlingtoni* Cochran). Of the three species, *monticola* was named on the basis of a single male from "the northern and eastern foothills, Massif de la Hotte, 1000-4000 feet, Haiti." Additional specimens of this species were reported by Williams from the general region about and to the north of Camp Perrin and from Ile Grande Cayemite off the north coast of the Tiburon Peninsula of southwestern Haiti. The third species (described as *A. darlingtoni* by Cochran, but later changed to *A. etheridgei* by Williams [1962], for nomenclatural reasons) was named from seven specimens collected by P. J. Darlington at four localities in the Cordillera Central of the República Dominicana. Finally, *A. christophei* from the Citadelle Laferrière in northern Haiti was based upon two females, both of which had been rather long in preservative. Williams (1962) reported on the coloration and pattern in life of *A. monticola,* and described the males of *A. christophei.* The latter species was still known only from the vicinity of the type locality. As for *A. etheridgei,* the coloration and pattern of this species were still unknown, and its range remained as delimited by the original holotype and paratypes.

The three species in the *monticola* group share a community of scale characteristics; those that distinguish them from other Hispaniolan anoles are the ventrals in transverse rows plus the

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subocular scales separated from the supralabials by a row of intervening scales (Williams, 1962:6). There is also agreement in other and more minor details of scalation, but the limits given by Williams (1962) for these data have been somewhat expanded by our examination of far more material than was available to him at the time of that paper.

Perhaps the most significant observation on the *monticola* group is that of Williams (1962:7), who stated that, "Whether there are any more members of this small sub-group of Hispaniolan anoles will have to be determined by more thorough search of the island . . . If related species are equally local in distribution, they may well have been missed." In the spring of 1966, Thomas secured a series of still another member of the *monticola* group in north-central Haiti, rather close to the type locality of *A. christophei*. Since we now have large series of the members of this group and much additional information on variation, distribution, and natural history, it is appropriate to summarize all of our data in the present paper and to describe the new northern Haitian species.

We are very grateful to Miss Patricia A. Heinlein, Donald W. Buden, Ronald F. Klinikowski and David C. Leber for assistance in the field in the República Dominicana. It also gives us very great pleasure to acknowledge Mr. Leber's work on our behalf in the careful execution of the color portraits reproduced herein; with three exceptions (the races of *A. monticola* and the new species) these were done in the field from living lizards. We most readily acknowledge the assistance of Ernest E. Williams in the present endeavor, not only for suggesting that we name the new species and for the loan of recently accumulated material in the Museum of Comparative Zoology of a group in which he is personally interested but also for his guiding our way through the at times impenetrable mass of Hispaniolan anoles. We have followed his techniques in taking of data and in description, so that the present information may be more readily compared with his own descriptions of several Hispaniolan anoles. Finally, Dr. Williams has graciously allowed that portions of a projected paper by himself and Schwartz be withdrawn and utilized herein, so that information on all the members of the *monticola* group might be more compactly available.

Our data are based primarily on specimens in the Albert Schwartz Field Series (ASFS), but we have also borrowed material from the Museum of Comparative Zoology (MCZ), the Field Museum of Natural History (FMNH), and the American Museum

of Natural History (AMNH); for the courtesy extended us in these matters, we wish to thank Ernest E. Williams, Robert W. Inger, Hymen Marx, Charles M. Bogert, and Richard G. Zweifel. Dr. Zweifel's assistance in supplying copies of pertinent field notes is also much appreciated. William G. Hassler kindly allowed us to examine his photographs and field sketches of some of the anoles concerned.

This study has been supported in part by National Science Foundation grant GB 2444 to Dr. Ernest Williams.

Anolis christophei Williams

The apparently most primitive member of the *christophei-etheridgei-monticola* trio of Hispaniolan anoles, *A. christophei,* was described from two female specimens from the Citadelle Laferrière, Dépt. du Nord, Haiti (Williams, 1960). Later, this description was amplified by a series of 20 additional specimens from the type locality (Williams, 1962). The species has thus been known only from topotypical specimens and its distribution has otherwise been unknown. In March 1963, four of these lizards were taken at Paraje La Palma, La Vega Province, República Dominicana, by C. E. Ray and R. Allen; the species was thus known to inhabit the eastern Cordillera Central as well as the Bonnet-a-l'Evêque in

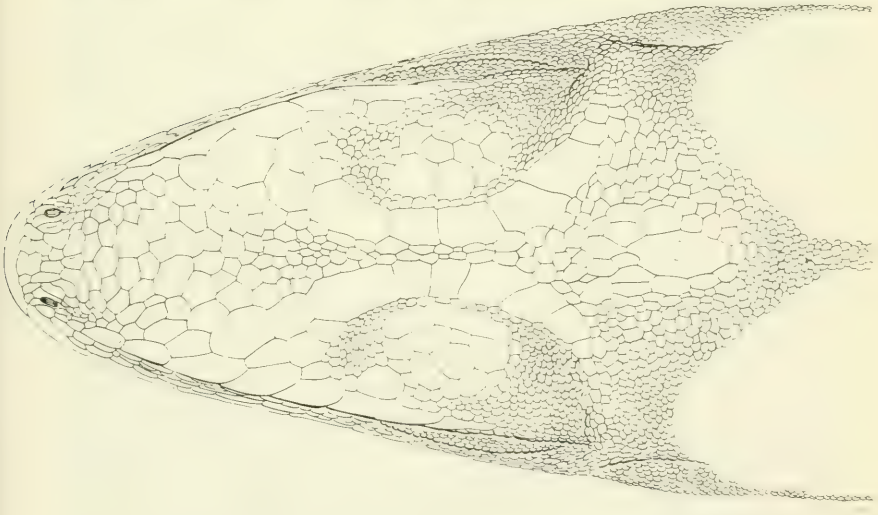


Figure 1. Dorsal view of head of *Anolis christophei,* ASFS X9193. Snout-vent length 45 mm.

the Chaine de Marmelade in the north. The elevation of the type locality is 2840 feet (865 meters); the elevation of the La Palma specimens is unknown. The coloration and pattern of *christophei* have not been described from living specimens; additional material collected by ourselves and associates in 1963, 1964 and 1966, and in 1964 by J. D. Lazell, Jr. has contributed information not only on these characters but also on the ecology and habits of the species.

A. christophei is now known to occur in four regions, and doubtless is distributed in the intervening areas, with one probable exception. It is a fairly common lizard in the Cordillera Central in the República Dominicana. Specimens have been collected from the northeast of Jarabacoa, south to west of Constanza, but not in the Valle de Constanza itself. Not only does the species occur in the uplands, but it is also to be found on the steep eastern escarpment of the Cordillera between El Río and Jayaco. Elevations of occurrence in this general area vary between about 2000 feet (610 meters) and 4250 feet (1296 meters) (Fig. 14). A second major area of occurrence is in San Cristóbal Province, near El Cacao. This locality lies on the southern slopes of the Cordillera Central; the lizards were taken at elevations of 1200 to 1400 feet (366 to 427 meters). The third area of occurrence is in the Cordillera Septentrional; at only one locality in this range, *A. christophei* was collected at an elevation of 2200 feet (671 meters). The final region whence *A. christophei* has been taken is the Chaine de Marmelade in Haiti, at elevations of 2840 feet (865 meters) to 3500 feet (1068 meters). The altitudinal distribution of the species is known to encompass elevations of from 1200 to 4250 feet (366 to 1296 meters) and its geographical distribution includes the Massif du Nord (presumably) in northern Haiti, the Cordillera Central in central and southern República Dominicana, and the Cordillera Septentrional in the northern portion of the latter country. The first three areas are presumably confluent, whereas the lizards in the Septentrional are apparently completely cut off from their southern and western relatives by the arid portion of the Valle de Cibao. It is barely possible that *A. christophei* occurs to the east in the República Dominicana and thus circumvents the inhospitable part of the Valle de Cibao, thereby bridging the apparent gap between the Cordillera and Septentrional populations. Certainly the valley of the Río Yuna is sufficiently mesic, and even now reasonably well forested, to support *A. christophei*. However, we consider it unlikely that these wet lowlands are presently inhabited by such a confirmedly montane lizard.

A. christophei, although observed with some frequency during the day, is much more readily collected at night. Most specimens were taken sleeping on ferns (especially tree-ferns), herbs, and shrubs along the margins of streams in gallery forest in the pine-clad uplands of the Cordillera Central. The greenish brown dorsal coloration renders them relatively inconspicuous under such circumstances, but the long dark almost filamentous tail often reveals their presence. The hindlimbs are flexed in the sleeping posture, and the lizards sleep more often across the leaflets and/or leaves rather than aligning themselves along the stems of branchlets; often they give the appearance of having been suddenly overtaken by the lowering temperatures of nightfall and of having stopped abruptly in their tracks. They give the impression of being draped across the greenery rather than having deliberately chosen a resting place for the night. This posture is in direct

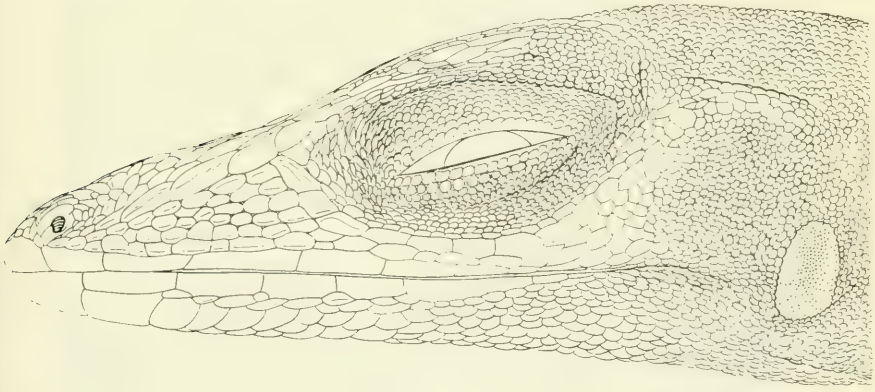


Figure 2. Lateral view of head of *Anolis christophei,* ASFS X9193. Snout-vent length 45 mm.

contrast to that of such larger anoles as *A. cybotes, A. distichus,* and *A. ricordi* which are encountered with them, but is quite similar to that of *A. etheridgei* which occupies similar situations at night.

The habitat of this anole is moist, shady, montane woods, particularly stream-associated forests and mesic ravines. During the day *A. christophei* was observed on tree trunks (four to six feet above the ground) along wooded edges of the Río Jimenoa below Paso Bajito, and on tree trunks and fallen but sloping logs near Paso Bajito itself. One was found on a fence post in riparian

woods near El Río. The Haitian specimens were collected in dense second-growth woods, where they were found on small trees, two to five feet above the ground. At night along a very narrow rivulet adjacent to a *platanal* east of El Río, *A. christophei* occupied the usual stream-side plants, and was not encountered on larger shrubs and trees nor on the banana plants themselves. The specimens from near El Cacao in the southern Cordillera Central were collected at night as they slept on bushes and ferns along the roadside in a region of coffee and cacao plantations. In the Cordillera Septentrional, specimens were also taken at night from stream-side shrubs and vines (the only place where they were encountered on the latter type of plants); on the vines, the lizards slept on the leaves and not on the woody stems. In no instance was there any attempt at concealment.

Perhaps the most noteworthy characteristic of *A. christophei* is the extremely large dewlap for so small and relatively slender a lizard (Pl. 1, *upper left*). The dewlap is pale, grayish purple (Pl. 47E2, Maerz and Paul, 1950, for Haitian specimens) or violet in life, with widely separated rows of pale yellow to whitish, or grayish, or bluish scales. The dewlap skin usually has a strangely metallic lustre which is distinctive. The dorsum is greenish brown to yellow-brown, with the heads distinctly greener than the back. There are four pairs of darker brown, bronzy or distinctly greenish brown paramedian blotches which often are fused across the midline of the back to give four butterfly-shaped figures between the shoulders and the sacrum. The spaces between blotches are not clear but are variously marbled or marked with darker green or brown, so that the whole effect is extremely cryptic. There is a yellow-green to yellow-buff shoulder stripe which continues down the sides as a vague, paler, lateral stripe. There is a yellow to greenish yellow subocular semicircle and a black to very dark brown postocular smudge. The chin and throat are dark gray; the ventral color is yellow to greenish yellow, and the tail is terminally black. In the dark phase, the dorsal ground color is dark gray with a purplish tinge, and the markings are very dark gray (nearly black) with a reddish or bronzy tinge. There is neither sexual dichromatism nor ontogenetic change in coloration or pattern; a single tiny juvenile (snout-vent length 21 mm) is colored and patterned like adults. The iris is blue. Although *A. christophei* is a small anole, it is not obviously slim and attenuate; the long tail adds to the impression of attenuation.

A. christophei is not strongly sexually dimorphic in size, although males reach a slightly larger size (49 mm snout-vent

length; ASFS X8835) than females (45 mm snout-vent length; ASFS V1957). There are 6 to 10 (mode 8) scales across the snout at the level of the second canthal, and 4 to 8 (mode 6) rows of loreals. The supraorbital semicircles are separated by one or two scales (mode 1), and there are 3 to 7 (mode 4) scales between the interparietal and the semicircles. Fourth toe lamellae on phalanges II and III vary from 18 to 25 (mode 22, with 16 specimens, but 15 specimens have 23 lamellar scales).

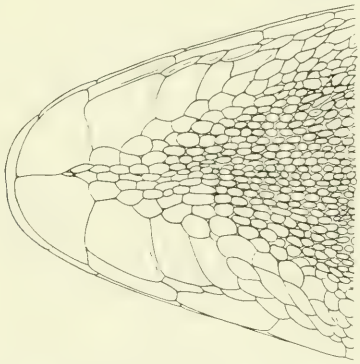


Figure 3. Mental region of head of *Anolis christophei,* ASFS X9193. Snout-vent length 45 mm.

Specimens examined: HAITI, *Dépt. du Nord,* Citadelle Laferrière, 20 (MCZ 66900-19); *Dépt. de l'Artibonite,* 8 to 9 km W Marmelade, 3500 feet (1068 m), 13 (ASFS V9900-12); REPUBLICA DOMINICANA, *La Vega Province,* Municipio Constanza, Paraje La Palma (not mapped), 15 (MCZ 75142-43, 79349-51, 79353-62); 6 km W Constanza, 4250 feet (1296 m), 2 (ASFS X8834-35); 11 km NE Jarabacoa, *ca.* 2000 feet (610 m), 6 (ASFS V4198-201, V4326-27); 10 km NE Jarabacoa, 1 (ASFS V4216); 4 km E Paso Bajito, Río Jimenoa, 2700 feet (724 m), 10 (ASFS X8850-57, V1866-67); 4 km SW El Río, 4000 feet (1220 m), 5 (ASFS X8552-55, X8737); 4 km SW El Río, 3500 feet (1068 m), 3 (ASFS X8886-88); 6 km E El Río, 3600 feet (1098 m), 7 (ASFS X9205-11); 7.1 mi. (11.4 km) E El Río, 3500 feet (1068 m), 1 (ASFS X8113); 23 km E El Río, 3050 feet (930 m), 3 (ASFS X9193-95); *Espaillat Province,* 2 km N Puesto Grande, 2200 feet (671 m), 6 (ASFS V1956-61); *San Cristóbal Province,* 15.5 km SE El Cacao, 1400 feet (427 m), 2 (ASFS V2498-99); 2.1 km SE El Cacao, 1200 feet (366 m), 6 (ASFS V2492-96, V2502).

ANOLIS ETHERIDGEI Williams

Anolis etheridgei Williams (= *Anolis darlingtoni* Cochran, 1939) was described from four localities in the Cordillera Central in the República Dominicana: Loma Vieja, south of Constanza; Loma Rucilla; Valle Nuevo; and Constanza. The included elevations for these four localities are from 3000 feet (915 meters) to 8000 feet (2440 meters). The type series comprised a total of seven specimens. From this it might be assumed that *A. etheridgei* is uncommon; this is far from the case since it is one of the more abundant anoles of these interior uplands, although its total distribution is still somewhat circumscribed and surely incompletely known. No previous information on coloration and pattern in life has been reported.

New specimens (three of which were taken by J. D. Lazell, Jr., in 1964, and the balance by ourselves and associates in 1963) indicate that the known distribution of *A. etheridgei* is confined to the interior highlands of the Cordillera Central in the República Dominicana, from Loma Rucilla on the west to east of El Río on the east, from Paso Bajito on the north to southeast of Constanza on the south (Fig. 14). Although one of the paratypes is recorded from Constanza (and this town is within the limits of the range of *etheridgei* as noted above), no additional specimens have

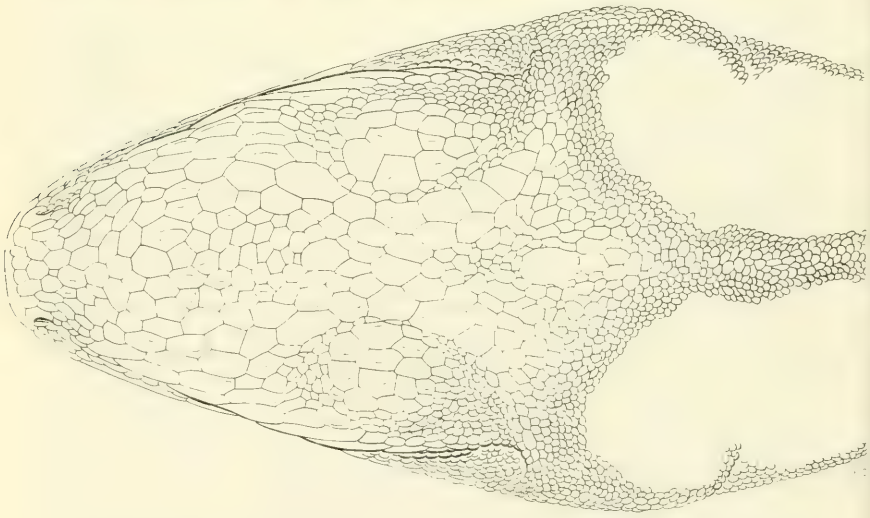


Figure 4. Dorsal view of head of *Anolis etheridgei,* ASFS X9146. Snout-vent length 42 mm.

been taken from the Valle de Constanza, despite careful search for it there. Recently collected specimens indicate an altitudinal range of 3050 feet (930 m) to 6100 feet (1890 m); these elevations are embraced by the data for the type series, although in almost every case of the latter, the elevation for each locality is an inclusive range.

A. etheridgei is similar to *A. christophei* in habitat preferences, and although it was encountered frequently sleeping on tree ferns, shrubs and herbs in gallery forest at night, it is not confirmedly restricted to this sort of situation. Specimens were collected in a protected and secluded depression (about 7 meters in diameter) in rainforest north of Constanza; the depression was protected by a dense thicket along its margins, and the lizards were sleeping on bushes in the center of the depression. During the day occasional specimens were encountered in forest on bushes or small trees adjacent to paths, but many more were observed and collected with facility while sleeping at night. The discussion of the sleeping habits of *A. christophei* applies equally well to *A. etheridgei*. Sleeping lizards are found draped over the leaflets of ferns and tree-ferns, the leaves of herbs and shrubs, and are not aligned along the branches or twigs. Their long tails reveal their presence with ease. None was encountered sleeping on vines, and usually the lizards were seen within two feet of the ground surface. The legs are flexed in the sleeping posture.

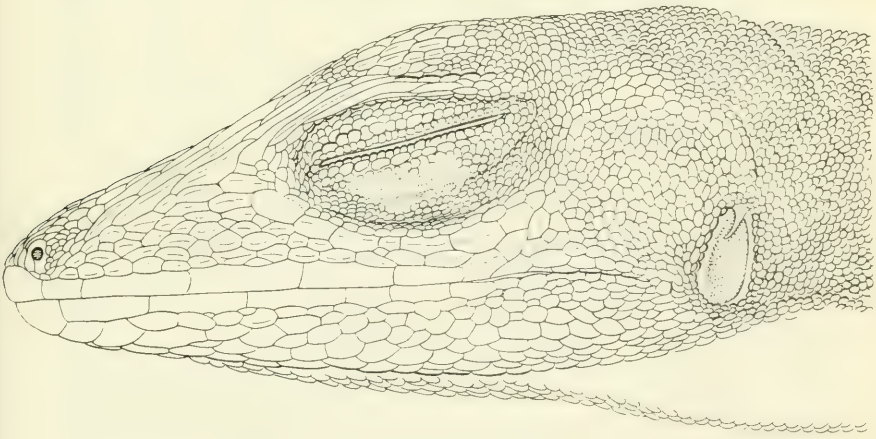


Figure 5. Lateral view of head of *Anolis etheridgei*, ASFS X9146. Snout-vent length 42 mm.

A. etheridgei, in contrast to *A. christophei,* is sexually dichromatic. Males are transversely crossbanded with four darker crossbands between the neck and sacrum. These bands may be fairly prominent or much obscured due to interband pigmentation. The neck is brown to bronzy above, with bright pea-green on the sides of the head and neck, blending into a duller green on the sides. The back is some shade of tan to brown, always dull in hue. The sides of the head and neck may be pale powder-blue rather than green. The ventral color is tannish opalescent to opalescent. The general coloration of males is a combination of tans, browns, and greens of varying hues. The dewlap is small, all white or white with a grayish basal area (Pl. 1, *upper right*). Females have a dorsal longitudinal bronzy zone, bordered dorsolaterally by rich dark brown longitudinal bands which extend onto the postorbital area. The dorsal bronzy band expands on the head and forms a U-shaped bronzy nuchal figure which abuts against the upper eyelids. Females at times have a series of four or five middorsal diamonds superimposed on the dorsal band; the halves of each diamond may be staggered to give a more complex dorsal pattern. The sides of the neck are white, and often females lack green or any greenish tints at all. The venters are like those of males except that occasional specimens have the venter light brown with a pinkish tinge. Both sexes have a cream subocular spot (which is more prominent in males) and the iris is blue. The chin and throat are very pale green in males and cream with brown striae in females.

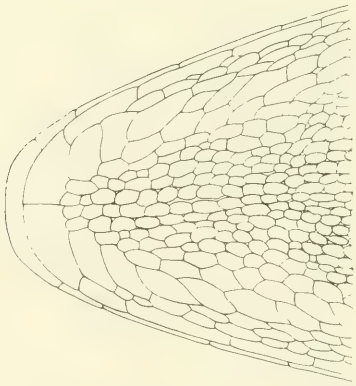


Figure 6. Mental region of head of *Anolis etheridgei,* ASFS X9146. Snout-vent length 42 mm.

Of the seventy-eight lizards available to us, the two largest males and the largest female (all with snout-vent lengths of 43 mm) come from a series of four lizards from 9.1 mi. (14.6 km) N of Constanza. Despite the long series from elsewhere in the Cordillera, strangely the three largest lizards are from the same small series; the difference in bulk of animals in this small lot of lizards, compared to those from elsewhere, was rather striking in life as well.

There are from 8 to 15 (mode 10) scales across the snout, and there are 5 to 10 (mode 6) rows of loreals. The scales between the supraorbital semicircles vary from 0 (semicircles in contact) to 4 (mode 2), and there are from 3 to 6 (mode 4) scales between the interparietal scale and the semicircles. Fourth toe lamellae on phalanges II and III vary from 15 to 21 (mode 18).

Specimens examined: REPUBLICA DOMINICANA. *La Vega Province*, Municipio Constanza, Paraje La Palma (not mapped), 3 (MCZ 79345-47); 7.2 mi. (11.4 km) S Constanza, 5000 feet (1525 m), 1 (ASFS X8241); Loma Vieja, 6000 feet (1830 m), south of Constanza, 1 (FMNH 73378); 12.6 mi. (20.2 km) SE Constanza, 6100 feet (1891 m), 1 (ASFS X9146); 16 km N Constanza, 6000 feet (1830 m), 1 (ASFS X8950); 9.1 mi. (14.6 km) N Constanza, 3500 feet (1068 m), 4 (ASFS X8791-94); 4 km SW El Río, 4000 feet (1220 m), 30 (ASFS X8522-51); 4 km SW El Río, 3500 feet (1068 m), 3 (ASFS X8889-91); 6 km E El Río, 3600 feet (1098 m), 1 (ASFS X9212); 23 km E El Río, 3050 feet (930 m), 14 (ASFS X9179-92); 22 km NW Bonao, 3900 feet (1189 m), 11 (ASFS V4282-92); 23 km NW Bonao, 4100 feet (1251 m), 1 (ASFS V4272); 19.6 km NE Bonao, 3300 feet (1007 m), 6 (ASFS V4296-301); 11 km E Paso Bajito, 4500 feet (1372 m), 1 (ASFS X8849).

Anolis monticola Shreve

In 1962 Williams reviewed the then available material of *A. monticola* and recorded its colors in life, based on notes taken by W. G. Hassler in 1935, and by A. S. Rand and J. D. Lazell in 1960. He then indicated that, on the basis of very recent material not included in that study, there appeared to be differences between populations of the northern and southern slopes of the Massif de la Hotte. Our own material, plus additional specimens (MCZ 74866-70), shows that there are indeed two forms of *monticola*: one possessing the four prominent dark ocellar patches as shown by Williams (1962: fig. 2), and one lacking the pair of nape patches.

Williams (1962) cited five specimens collected by W. G. Hassler (AMNH 49818, 49845, 50108-09, MCZ 65139, formerly AMNH 50110) with the locality given as "25 miles north of Aux Cayes on Jeremie Road" and MCZ 56140 from "mountains on Jeremie road about 8 miles from Camp Perrin." Reference to the map of Haiti published by the Service de Géodésie et Cartographie 1:100,000 shows that 25 miles north of Les Cayes lies well onto the northern slope, as does the locality 8 miles from Camp Perrin. We have consulted Hassler's original field notes and find that the true situation is otherwise: AMNH 49845 is in actuality listed as being from "high Mts. on Jeremie road 32 miles from Aux Cayes 2000-3000′ approx."; AMNH 49818, 50108-10 are said to be from "about 4 miles from Camp Perrin." It is thus evident that these localities have suffered in the transcription to the catalogue.

The specimens from 4 miles north of Camp Perrin are from the south slope, if the distance is accurate; the Tombeau Cheval specimens cited by Williams, 1962, are apparently from south of the high point on the Jérémie road but near it. The specimens of these two series agree in having the four ocellar patches.

Recent material from farther west, obtained by Thomas, lacks the nape ocellar patches and agrees in this respect with MCZ 74866-70 from Trou Bois, 1½ miles south of Beaumont on the Les Cayes-Jérémie road, and with AMNH 49845 from 32 miles from Les Cayes on the Jérémie Road (which is probably in the vicinity of the locality for the Trou Bois series). The type specimen of *monticola,* although with the color pattern obscured by preservation and age, lacks the pair of nape patches (the neck patches and dorsal dark bands can still be seen), and thereby agrees with the material just mentioned. The locality for this specimen is not precisely known, but "northern and eastern foothills of the Massif de la Hotte" is in reality the northern and eastern foothills of Pic Macaya (P. J. Darlington, pers. comm. to E. E. Williams), the highest peak of the range, which lies to the west of the Tombeau Cheval region (Fig. 10). We are convinced that two distinct populations of *Anolis monticola* have been sampled: one, of the northwestern and western extreme of the Massif de la Hotte, and another farther to the east (and possibly to the south).

We regard the Grande Cayemite record for *monticola* (MCZ 58026, a female, collected by W. J. Eyerdam) as dubious. Thomas has visited this island and the habitat is for the most part very arid, not at all similar to habitats occupied elsewhere by *monticola.*

This is not in itself incontrovertible evidence against the occurrence of the species on that island, and it may be noted that *Diploglossus sepsoides* Gray, normally an inhabitant of distinctly moist situations, does occur there. However, the single Eyerdam specimen of *Sphaerodactylus copei* Steindachner was noted as being indistinguishable from *S. copei picturatus* Garman from the nearby mainland (Schwartz and Thomas, 1964:326), yet the recently obtained series of *S. copei* from Grande Cayemite is undeniably a distinctive new subspecies. The Eyerdam collection is also responsible for the aberrant locality of the Citadelle Laferrière for specimens of *Anolis hendersoni* Cochran (Williams, 1963), a trenchantly south island species. We will not be apodictic but regard the Grande Cayemite specimen with suspicion.

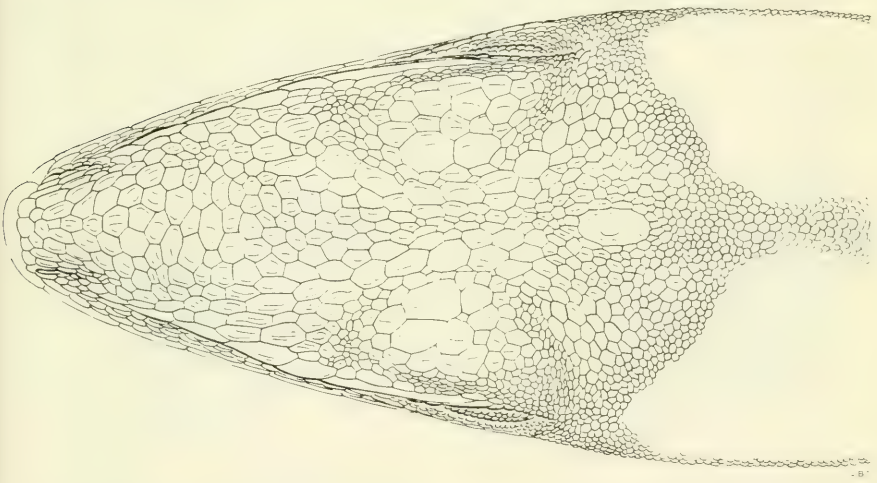
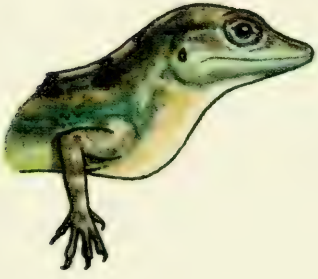


Figure 7. Dorsal view of head of *Anolis monticola quadrisartus,* type, MCZ 62998. Snout-vent length 43 mm.

Anolis monticola shows strong sexual dimorphism in size; males reach a maximum of 55 mm and females 39 mm. There are 7-11 (mode 9) scales across the snout at the level of the second canthal and 6-9 (mode 7) loreal rows. The supraorbital semicircles are separated by 2-4 (mode 3) scales, and there are 3-6 (mode 4) scales between the interparietal and the semicircles. Fourth toe lamellae in phalanges II and III vary from 17-21 (mode 18 or 19).

Plate 1. Lateral views of heads of males of four species of Hispaniolan *Anolis,* as follows: *upper left, Anolis christophei,* ASFS X8113, 7.1 mi. E El Río, La Vega Prov., República Dominicana, painted from living specimen; *upper right, Anolis etheridgei,* ASFS X8522, 4 km SW El Río, 4000 feet, La Vega Prov., República Dominicana, painted from living specimen; *center left, Anolis monticola monticola,* ASFS V9624, *ca.* 5 km SSE Marché Léon, Dépt. du Sud, Haiti, painted from Thomas' field notes and color transparencies of living specimens; *center right, Anolis monticola quadrisartus,* MCZ 63004, paratype, Tombeau Cheval, Dépt. du Sud, Haiti, painted from color noted by collectors, as quoted by Williams (1962:3-4); *lower, Anolis rimarum,* AMNH 96469, paratype, 8 to 9 km W Marmelade, Dépt. de l'Artibonite, Haiti, 3500 feet, painted from Thomas' field notes on living specimens.



Anolis monticola monticola Shreve

Diagnosis: A subspecies of *Anolis monticola* characterized by the absence of paired, large, black, light-centered ocelli on the nape, and by a yellow to reddish orange dewlap; females have a relatively straight-sided (in contrast to wavy or scalloped) middorsal zone.

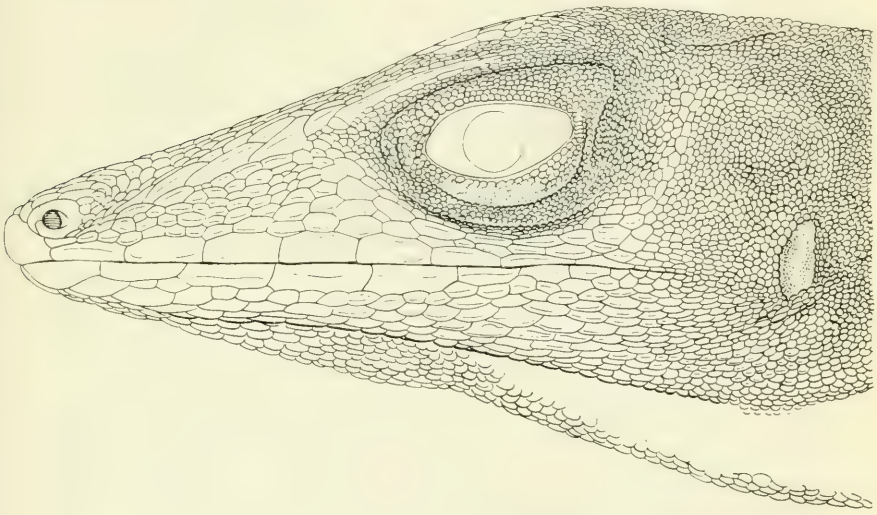


Figure 8. Lateral view of head of *Anolis monticola quadrisartus,* type, MCZ 62998. Snout-vent length 43 mm.

Color in life: The dorsal ground color of males is dull greenish yellow middorsally; the sides are brighter yellow-green to yellow-brown. The labials and the sides of the neck have an indistinct pastel blue to blue-green stripe. The saddles and the nuchal spots are black, and the ocelli in the nuchal spots are bright blue. The venter is faintly greenish yellow. The throat is blue to blue-green, becoming yellowish centrally. The dewlap is yellow to reddish orange (Pl. 1, *center left*). The limbs are greenish yellow with some brown suffusion and banding, and the tips of the digits, and palmar and plantar surfaces, are black. The nominate form is also known to assume a gray to brown ground color phase dorsally, with black markings and little or no bright dorsal color. The ground color of the sides below the middorsal zone may also be pale translucent green. The dark dorsal saddles continue diagonally and posteriorly below the middorsal zone and are much

invaded by light color, to the extent of appearing split longitudinally and giving the effect of trailing off. The ocelli in the black patches may be single and relatively large or multiple and smaller. The color portrait was executed from this information.

Females are duller than males and have a simpler zonate pattern of a light (brown), relatively straight-edged middorsal zone (usually with only one or two small undulations), and darker sides.

Habitat: 1) *ca.* 7 km (airline) WSW Moron. This locality is in the foothills of the limestone massif (Monts Cartaches) of the northwestern Tiburon Peninsula. Specimens were collected on a hillside and ravine side of limestone rocks and boulders with mesic vegetation of coffee, some bananas, and a high shade cover of breadfruit and other trees. Specimens were seen only in shady areas, mostly in coffee, where they were found on rocks and ground and sometimes on low (usually dead and fallen) branches and twigs. They were most abundantly found in an area (a small ravine) which had low herbaceous plants covering the ground, where they appeared to be foraging. (The time of the visit to this locality was between 0900 and 1000.) These anoles were very agile and retreated, almost invariably, into rock crevices when pursued. Many more were seen than were collected. 2) *ca.* 10 km WSW Moron, 1500 feet (456 meters). This was a steep hill slope to the west of the road, the opposite side of which was covered with a dense almost rain forest-like vegetation; specimens of *monticola* were seen around some rock outcroppings in the wooded area. Five were collected. 3) *ca.* 5 km (airline) SSE Marché Léon, 2600 feet (793 meters). Specimens were collected in a ravine filled with a jumble of limestone boulders and overgrown with mesic vegetation; the surrounding area was much cut over. 4) *ca.* 8 km (airline) S Marché Léon, 3000 feet (915 meters) (Castillon). No specimens of *monticola* were collected but many individuals were seen along the base of a hillside covered with slabs and fragments of limestone; the area was relatively open and without heavy shade, although with some ground vegetation, in contrast to other localities where this species was seen. An adjacent hillside on the opposite side of a ravine and stream had no extensive outcroppings of rock, and nowhere on this hillside, even in a few places where vegetation was moderately thick, were examples of *A. monticola* seen.

Specimens examined: HAITI, *Dépt. du Sud:* ASFS V9196-211, *ca.* 7.5 km (airline) WSW Moron; ASFS V9270-74, *ca.* 10 km (airline) WSW Moron, 1500 feet (456 m); ASFS V9624-26, *ca.* 5

km (airline) SSE Marché Léon, 2600 feet (793 m); MCZ 74866-70, Trou Bois, about 1½ km S of Beaumont, on Jérémie road; MCZ 38296 (type), northern and eastern foothills, Massif de la Hotte (= Pic Macaya), 1000-4000 feet (305-1220 m); AMNH 49845, high in mountains on Jérémie road 32 miles from Les Cayes, 2000-3000 feet (610-915 m) approx.; MCZ 65026, "Grande Cayemite."

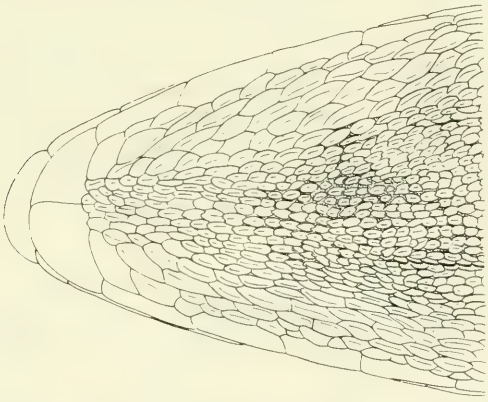


Figure 9. Mental region of head of *Anolis monticola quadrisartus,* type, MCZ 62998. Snout-vent length 43 mm.

Anolis monticola quadrisartus[1] new subspecies

Holotype: MCZ 62998, collected at Tombeau Cheval between Camp Perrin and Beaumont, Dépt. du Sud, Haiti, by A. S. Rand and James D. Lazell, Jr., 7 August 1960.

Paratypes: MCZ 62999, 63001-04, same data as type; AMNH 50108-09, AMNH 49818, MCZ 65139, about 4 miles from Camp Perrin, Dépt. du Sud, Haiti.

Diagnosis: A subspecies of *A. monticola* characterized by a pair of black, light-centered ocelli on the nape in addition to the pair on the neck, and a blue to bright yellowish green dewlap (Pl. 1, *center right*). Females have edges of middorsal zone undulating and scalloped.

Coloration: Like that of the nominate race except for the diagnostic characters noted above. See Williams (1962) for color notes from specimens in life on the type series of *quadrisartus;* these notes also served as the source for the color portrait.

[1] From the Latin, meaning "patched four times."

Range: Known definitely only from the type locality (see discussion under the species above); possibly it is a race of the eastern La Hotte, or possibly of the southern slopes, although the present data do not indicate the latter (Fig. 10).

Habitat: Apparently identical to that of the nominate race; see Williams (1962) for habitat notes on the type series.

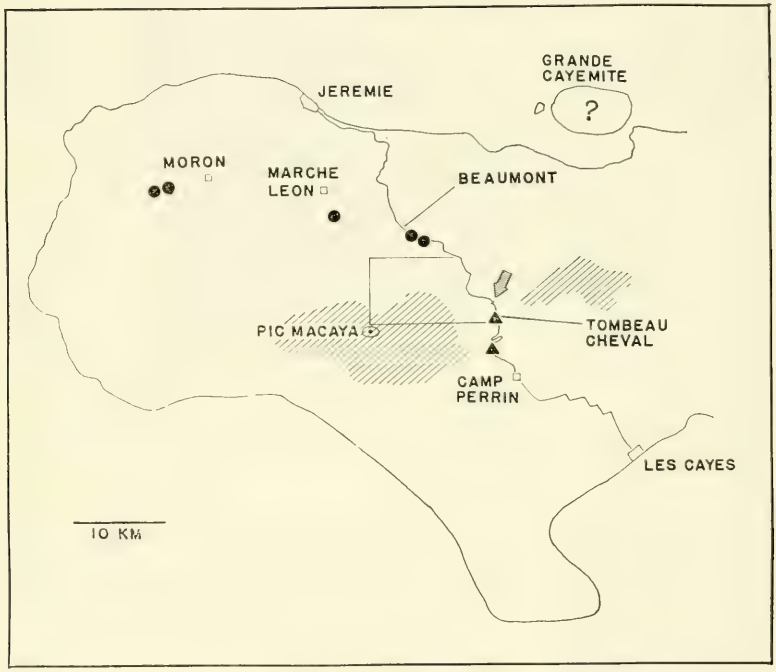


Figure 10. Tip of the Tiburon Peninsula, Haiti, showing distribution of the subspecies of *A. monticola,* as follows: circles indicate locality records for *A. m. monticola;* triangles, locality records for *A. m. quadrisartus.* Line connecting Les Cayes and Jérémie indicates road. Arrow indicates highest point (840 meters) along road. Hatched areas approximate regions above 1000 meter line. Large rectangle indicates northern and eastern foothills, Pic Macaya.

ANOLIS RIMARUM[1] new species

Holotype: MCZ 81128, an adult male, one of a series collected 8 to 9 km (airline) W of Marmelade, Dépt. de l'Artibonite, Haiti, at an elevation of 3500 ft. (1068 m), 2 April 1966, by Elie Cyphale and Richard Thomas. Original number ASFS V9896.

Paratypes: AMNH 96469-70, ASFS V9886-91, ASFS V9898, MCZ 81129, USNM 157914-16, same data as type.

Diagnosis: An anole of the Hispaniolan *christophei-etheridgei-monticola* assemblage distinguished by: smooth dorsal head scales; smooth, squarish supraoculars; a "window" of enlarged squarish palpebral scales; a nearly vestigial dewlap; smooth, juxtaposed ventrals arranged in transverse rows; transversely enlarged anterior femoral scales; somber coloration (browns, yellow-browns, dull greens); and black digits.

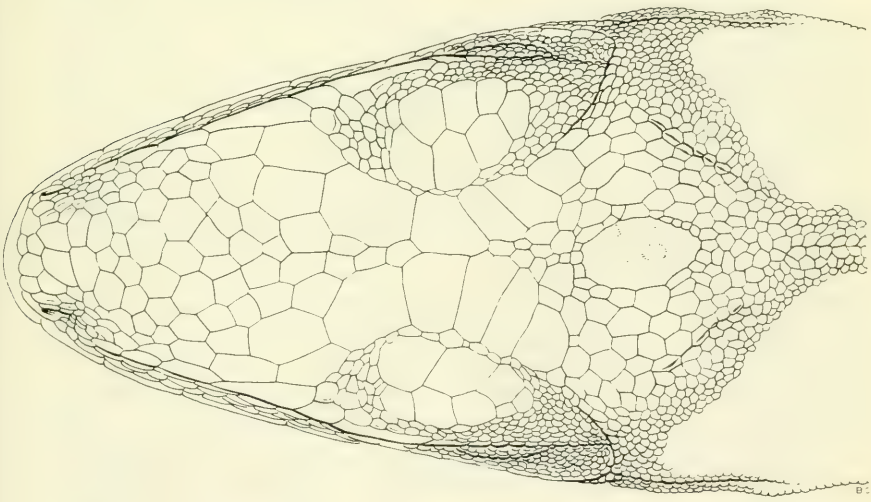


Figure 11. Dorsal view of head of *Anolis rimarum*, type, MCZ 81128. Snout-vent length 43 mm.

Description of type (variations of paratypes in parentheses): Head moderate, not especially elongate, snout pointed, slightly concave. Head scales smooth, at most with feeble keels; 7 (7-10) scales across snout at level of second canthal. Frontal depression

[1] From the Latin, *rima*, a crevice.

shallow. Anterior nasal scale in contact with rostral. Supraorbital semicircles narrowly in contact (also in six paratypes; separated in seven), separated from supraocular disks by one row of granules (rarely in narrow contact). Supraocular disks composed of about 7 enlarged, smooth, or only very faintly keeled scales and separated from supraciliary scales by 3 (3-4) rows of granules. Supraciliaries end at level slightly posterior to mid-eye, continued posteriorly by double row of slightly enlarged granules. Canthus rostralis distinct, sharp-edged, canthal scales 5-7. Loreal rows 5 (4-6), lower row largest. Temporals granular, supratemporals only slightly enlarged and with small granules between them and enlarged scales around interparietal. Interparietal large, about size of ear opening, separated from supraorbital semicircles by 2 (2-3) scales. Suboculars in contact with supralabials. Five supralabials to center of eye. Lower eyelids with window of enlarged squarish scales. Mental broader than long, in contact posteriorly with 3 (2-4) gular scales. Infralabials narrow, in contact with first enlarged sublabial; sublabials continue posteriorly as moderately enlarged row (or may blend completely with other scales of lateral gular region). Throat granules small, swollen, weakly keeled, slightly elongate anteriorly.

Trunk: Dorsal scales very small, granular, two middorsal rows enlarged; adjacent rows reduce gradually to normal flank scale size. Ventrals smooth, enlarged, squarish, juxtaposed and arranged in transverse rows.

Dewlap: Very small, principally confined to area between forearm insertion and angle of jaw, scales smooth, swollen, rounded, about size of ventrals or slightly larger (Pl. 1, *lower*).

Limbs and digits: Scales of upper surface of limbs imbricate, keeled; those of hands and feet multicarinate; one scale row of prefemoral surfaces, especially distally and onto knee, much enlarged transversely and multicarinate. Subdigital lamellae 18 (16-23).

Tail: Compressed, 4 middorsal scales per verticil. One pair of postanal scales well developed in males.

Size: Holotype, a male, 43 mm snout-vent (largest male 45 mm; largest female 40 mm).

Color in life: The dorsal ground color is gray-brown with a pattern of four gray to black middorsal butterfly markings or wide transverse bands that fade out on the lower sides; a coppery tinge is present on the middorsal line. The head is gray-brown dorsally with olive-green temporal stripes that meet on the occiput; another more ventral olive-green postocular stripe proceeds onto

the neck and fades out. The ground color of the lower sides of the head, neck and flanks is pale yellow-green with olive-green markings, including dark edges to the longitudinal flank stripes and other small dashes and vermiculations which may be present. The chin is whitish, as is the retracted dewlap (due to crowding of scales); the venter is pale metallic yellow-green. The dewlap skin is dull greenish orange (about pl. 13 L7, Maerz and Paul, 1950). The tail is dull yellow to orange, sometimes greenish on its basal half to two-thirds, and black distally. The digits of both hands and feet are black. The iris is pale blue and the lower eyelid is blue. Sexual dichromatism is not pronounced; the middorsal light stripe of females is broader and more conspicuous than that of males, and the lateral stripe is also more prominent. These color data were employed in making the portrait of *A. rimarum*.

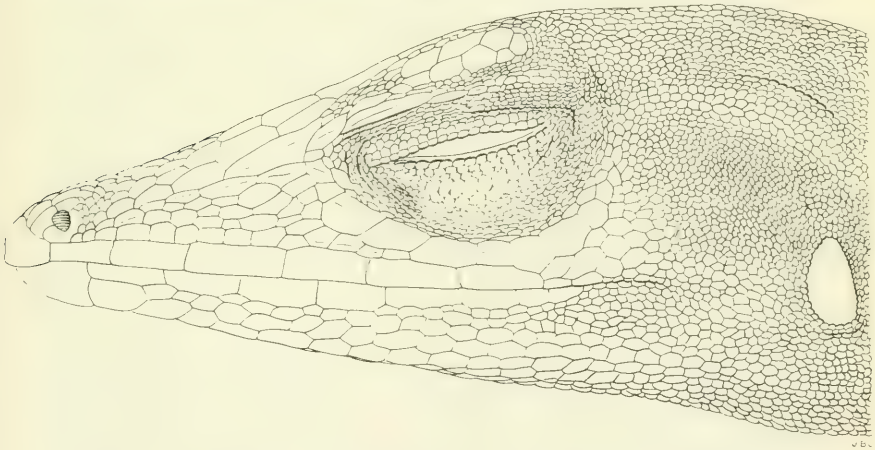


Figure 12. Lateral view of head of *Anolis rimarum*, type, MCZ 81128. Snout-vent length 43 mm.

Habits and habitat: The type series of *A. rimarum* was collected in a steep, limestone boulder jumble, a talus formation near the crest of the Chaine de Marmelade. The area (only a few acres in extent) was covered with a dense, natural, second-growth woods, mostly of small trees, brush and viny tangles but also with some moderately large trees. The specimens were found on rocks, low twigs and branches, and occasionally near the ground on the trunks or exposed roots of trees. They were seen most abundantly in areas where there was little thick undergrowth but

where there was considerable shade from taller plants. When approached, the lizards retreated with agility into rock crevices; many more were seen than were collected. The situation and habits of these anoles were virtually identical to those of *A. monticola.*

At precisely the same locality, *A. christophei* was also taken; specimens were found on the trunks of small trees about 2 to 5 feet above the ground. Less than half a kilometer to the west, *A. christophei* was taken from trees along the banks of a small ravine; the area was not rocky, and no examples of *A. rimarum* were seen.

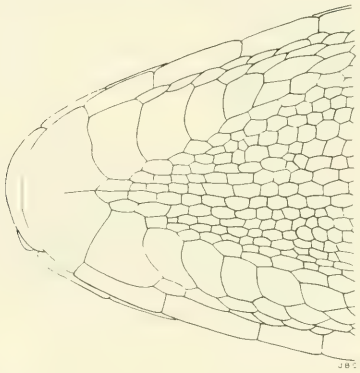


Figure 13. Mental region of head of *Anolis rimarum,* type, MCZ 81128. Snout-vent length 43 mm.

Comparisons: See Table 1 for a comparison of the diagnostic morphological characters of *rimarum, etheridgei, monticola* and *christophei.* Of these four anoles, *christophei* is the most divergent and, if truly a member of this group, is possibly the most primitive (Williams, 1962:7). Among the other three (*rimarum, etheridgei,* and *monticola*), there is nothing in the way of clear-cut alliances; any two share certain characters, and each species has certain peculiarities of its own. *Rimarum* seems to have more scale characters special to itself than *etheridgei* or *monticola* (Table 1:6, 8, 11, 12, 13, 14). All four species show certain similarities in body coloration, the basic pattern being that of dark crossbands or butterfly markings on a brown or gray ground color. *A. rimarum* may have either solid crossbars or butterfly markings; *christophei* has butterfly markings only. *Christophei* and *rimarum* are also similar in lacking strong sexual dichromatism (*rimarum* is slightly dichromatic; *christophei* is not); *monticola* and *etheridgei* are both

strongly dichromatic and dimorphic in size. In dewlap color, although not in dewlap size, *rimarum* and *monticola* are similar, both having some shade of orange as part of the variation; *etheridgei* has a whitish dewlap. The dewlap of *christophei,* which is altogether different from those of the others in size and scalation, has a purplish color. *Rimarum* and *monticola* are additionally similar in coloration in having black fingers and toes. *Monticola* is the most distinctive chromatically of the lot in having brighter colors and large, bold ocellar patches on the neck; *etheridgei* is next to *monticola* in brightness of coloration. The two agree further in the type of body banding: solid middorsally but trailing off into hollowed and punctulate bands on the sides.

In habits, however, *monticola* and *rimarum* appear identical in being inhabitants of boulder jumbles overgrown with low vegetation, where the lizards seek refuge in crevices. In contrast, the other two are tree (*christophei*) or tree and bush (*etheridgei*) anoles, also of forested areas.

Geographically, *monticola* is quite isolated from the other members of this group. The remaining three species are all inhabitants of the north island, *etheridgei* and *rimarum* being allopatric as far as is known, whereas the distribution of *christophei* encompasses the ranges of both.

In conclusion, we cannot offer a reasonable certain evolutionary analysis of this radiation of small Hispaniolan anoles. We follow Williams (1962) in regarding *christophei, etheridgei,* and *monticola* as members of a single assemblage; *christophei* is the most aberrant but agrees in general with the other three in habitus, dorsal coloration, blue iris color, and ventral squamation. We add *rimarum* to the group and note that it does little to bridge the gap between *christophei* and the others, although in some characters *christophei* and *rimarum* are slightly more similar to one another than to *etheridgei* and *monticola* (lack of sexual dichromatism, enlarged second canthal scale, generally smooth head scales.)

Williams (1962:7) pointed out the inverse relationship between dewlap prominence and boldness of dorsal pattern in male *monticola,* and remarked on the possible significance of this in maintaining species recognition. We do not deny that there may be such causal connection between boldness of dorsal pattern and prominence of dewlap in some cases, but we note that *rimarum* has the smallest dewlap (albeit brightly colored) of this group of anoles and also a relatively dull pattern. *A. etheridgei* has a somewhat brighter coloration than *rimarum* and

a larger but much less brightly colored dewlap. *A. christophei* has a dull dorsal coloration and a relatively dull dewlap (purplish) which is nonetheless distinctive because of its isolated rows of scales and its metallic hue. The presence of an incipient "window" of flattened translucent scales in the lower eyelid of *rimarum* and, to a lesser extent, in *monticola* supports the "sunglasses" theory proposed by Williams and Hecht (1955) to explain similar but more highly developed structures in two Cuban anoles (*A. argenteolus* and *A. lucius*). Both *rimarum* and *monticola* are inhabitants of shaded areas and, additionally, are associated with rocky crevices — conditions that may well be favorable to the development of a protective filter for the eyes.

LITERATURE CITED

Cochran, Doris M.

1939. Diagnoses of three new lizards and a frog from the Dominican Republic. Proc. New England Zool. Club, **18**: 1-8.

Maerz, A., and M. Rhea Paul

1950. A dictionary of color. New York, McGraw-Hill Book Co., pp. i-vii, 1-23, 137-208, 56 pls.

Schwartz, Albert, and Richard Thomas

1964. Subspeciation in *Sphaerodactylus copei*. Quart. Jour. Florida Acad. Sci., **27**(4): 316-332.

Williams, Ernest E.

1960. Notes on Hispaniolan herpetology. 1. *Anolis christophei*, new species, from the Citadel of King Christophe, Haiti. Breviora, Mus. Comp. Zool., No. **117**: 1-7.

1962. Notes on the herpetology of Hispaniola. 7. New material of two poorly known anoles: *Anolis monticola* Shreve and *Anolis christophei* Williams. Breviora, Mus. Comp. Zool., No. **164**: 1-11.

1963. Notes on Hispaniolan herpetology. 8. The forms related to *Anolis hendersoni* Cochran. Breviora, Mus. Comp. Zool., No. **186**: 1-13.

Williams, Ernest E., and Max K. Hecht

1955. "Sunglasses" in two anoline lizards from Cuba. Science, **122** (3172): 691-692.

(Received 2 August, 1966.)

Anolis christophei

1. Snout most elongate, most concave.
2. Canthus pronouncedly sharp-edged.
3. Scales 6-10 (mode 8) across snout at level of second canthal.
4. Loreal rows 4-8 (mode 6).
5. Scales in frontal depression numerous, polygonal to rounded, smooth or slightly rugose.
6. Supraoculars moderate to small in size, somewhat elongate, weakly keeled, *ca.* 9-11 in number.
7. Supraorbital semicircles keeled, separated by 1-2 scales (Fig. 1).
8. Lower eyelid covered with granules, without "window" of squarish scales.
9. Anterior canthal scales abruptly smaller.
10. Ventrals rounded to squarish, smooth, slightly imbricate and arranged in transverse rows.
11. Dewlap very large, extending from mid-gular region to mid-venter; scales at edge of dewlap smooth, imbricate, larger than ventrals.
12. Anterior femoral scales keeled, imbricate, not tranversely enlarged.
13. Interparietal small, *ca.* ½ or less size of ear opening.
14. Scales between interparietal and supraorbital semicircles 3-7.

Anolis etheridgei

1. Snout bluntest, not pronouncedly concave.
2. Canthus distinct but not prominently sharp-edged.
3. Scales 8-15 (mode 10) across snout at level of second canthal.
4. Loreal rows 5-10 (mode 6).
5. Scales in frontal depression numerous, polygonal, keeled.
6. Supraoculars small to moderate, slightly elongate, keeled, *ca.* 11 in number.
7. Supraorbital semicircles keeled, separated by 0-4 scales (Fig. 4).
8. Lower eyelid covered with granules, without "window" of squarish scales.
9. Anterior canthal scales not abruptly smaller.,
10. Ventrals rounded to squarish, subimbricate, smooth and in transverse rows.
11. Dewlap, small, extending from mid-gular region onto chest, scales keeled.
12. Anterior femoral scales keeled, imbricate, only slightly enlarged distally.
13. Interparietal small, less than ½ size of ear opening.
14. Scales between interparietal and supraorbital semicircles 3-6.

Anolis monticola	*Anolis rimarum*
1. Snout elongate, somewhat concave.	1. Snout elongate, somewhat concave.
2. Canthus sharp-edged.	2. Canthus sharp-edged.
3. Scales 7-11 (mode 9) across snout at level of second canthal.	3. Scales 7-10 (mode 8) across snout at level of second canthal.
4. Loreal rows 6-9 (mode 7).	4. Loreal rows 4-6 (mode 5).
5. Scales in frontal depression numerous, polygonal, keeled.	5. Scales in frontal depression reltively few, polygonal, pavimentous.
6. Supraoculars moderate in size, elongate, prominentaly keeled, *ca.* 9 in number.	6. Supraoculars large, not elongate, smooth or only faintly keeled, *ca.* 5-7 in number.
7. Supraorbital semicircles prominently keeled, separated by 2-4 scales (Fig. 7).	7. Supraorbital semicircles smooth or feebly keeled, in contact or separated by one scale only (Fig. 11).
8. Lower eyelid with "window" of small flat granules.	8. Lower eyelid with "window" of enlarged squarish scales.
9. Anterior canthal scales not abruptly smaller.	9. Anterior canthal scales abruptly smaller.
10. Ventrals acute to rounded, imbricate, keeled, and in transverse rows but not so diagrammatically as in others.	10. Ventrals squarish, juxtaposed to subimbricate, smooth and in transverse rows.
11. Dewlap small, extending from mid-gular region onto chest, scales keeled.	11. Dewlap very small, occupying only the region between the angle of the jaw and the chest, scales smooth, imbricate.
12. Anterior femoral scales imbricate, multicarinate but not transversely enlarged.	12. Anterior femoral scales transversely enlarged, feebly multicarinate.
13. Interparietal usually small, *ca.* ½ size of ear opening but may be equal to ear opening in size.	13. Interparietal large, about size of ear opening.
14. Scales between interparietal and supraorbital semicircles 3-6.	14. Scales between interparietal and supraorbital semicircles 2-3.

Table 1. Comparison of the four species of the *monticola* group of Hispaniolan anoles.

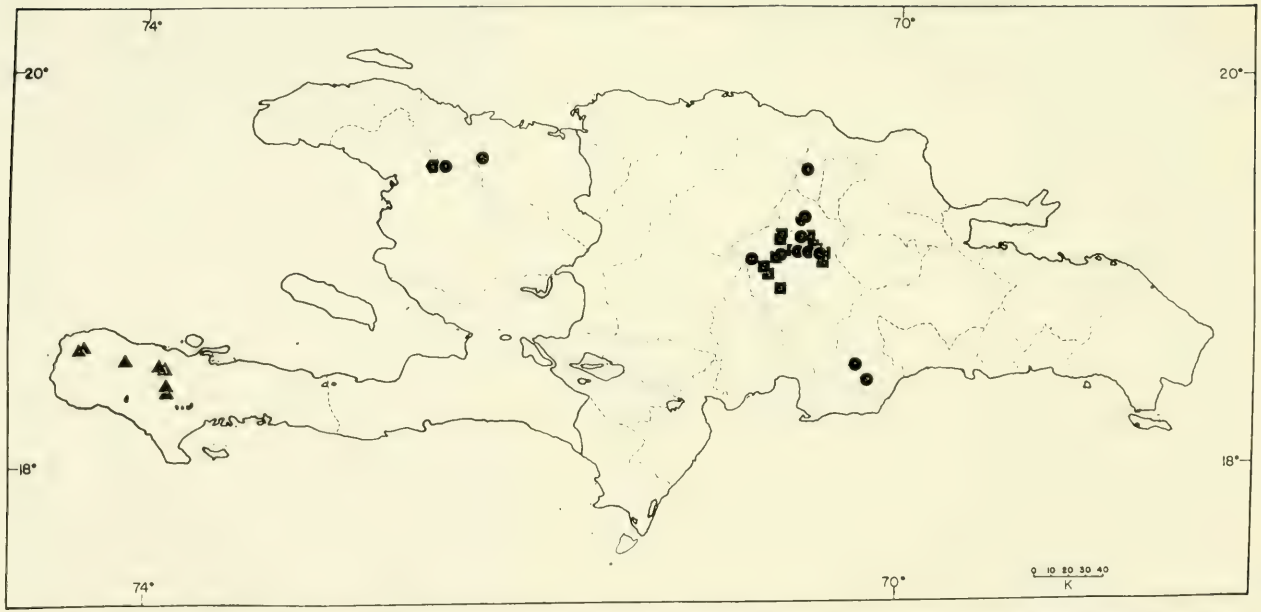


Figure 14. Hispaniola, showing locality records for the four species of the *Anolis monticola* group, as follows: *A. christophei,* circles; *A. etheridgei,* squares; *A. monticola,* triangles; *A. rimarum,* hexagon.

B R E V I O R A

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A PHYLOGENETIC SURVEY OF MOLLUSCAN SHELL MATRIX PROTEINS

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INTRODUCTION

Recent advances in biochemistry and cytology have vastly increased the availability of structures suited for phylogenetic research. Diverse and complicated chemical structures, such as cytochrome c (Margoliash and Smith, 1964) and chromosomes (Spencer, 1949), are amenable to a type of analysis based on formal properties analogous to that of traditional comparative anatomy. The growth of evolutionary biology has recently brought about a subtle, yet pervasive and fundamental, revolution in the aims and methods of systematics. The development of new techniques based on an understanding of the causes of evolution has so far been most pronounced in the study of species and speciation, but is being extended to higher levels (Cain, ed., 1959; Bock, 1959, 1960). The present work is an attempt to continue these trends, employing a new type of evidence made available by improved methods

[1] Contribution No. 91 from the Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, and Contribution No. 1834 from the Woods Hole Oceanographic Institution.

of chemical analysis: the proteinaceous matrix which serves as a framework for the calcareous portion of the molluscan shell. The preliminary survey discussed here is a methodological experiment, evaluating the feasibility of new techniques (logical, chemical and statistical). It appears, from both the consistency of the results and reference to traditional comparative anatomy, that the approach used here is useful for classification. Until more data are collected, however, the detailed conclusions should be considered tentative.

The development of these techniques has depended upon an interdisciplinary approach which has allowed efficient use of the data that otherwise would have been impossible. Systematic methods and results are stressed in this account. A fuller discussion of the chemical aspects of the study is being published elsewhere (Degens, *et al.,* 1966). A publication (Degens and Spencer, 1966) giving raw data and details of analytical techniques and computer methods is available on request.

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Responsibility for content rests with the authors, although valuable suggestions were provided by John Allen, Melbourne R. Carriker, Vida C. Kenk, Howard Sanders and Ruth D. Turner.

Drawings are by Ruth von Arx.

ANATOMICAL AND CHEMICAL BACKGROUND

The molluscan shell (cf. Wilbur, 1964; Glimcher, 1960) is produced by secretion of precursors from the epithelial tissue in specialized areas of the mantle, and may consist of several layers. The outer layer, or periostracum, is not calcified; it is thought to consist of quinone-tanned protein (Brown, 1952). The inner

layers are calcareous, and include a proteinaceous matrix which serves as a nucleation site for specific cations and anions, and in which the mineral crystals are deposited. The crystalline structure (Bøggild, 1930) and protein configurations (Grégoire, 1961) are quite intricate, suggesting a highly organized system. In mollusks, the uncalcified matrix is laid down extracellularly; only after the matrix has been formed is inorganic material from the underlying tissue incorporated into the shell.

We have been guided by the hypothesis that the shell matrix is derived from at least one structural protein which originally had some function other than that which it now serves. It seems reasonable that the evolution of a new function has occurred gradually. With the change from a non-calcified to a calcified state, the protein should become increasingly reorganized, so as to facilitate the effective binding and interconnection of the parts. In general, this should involve a proportionate increase in the amount of those organic components which facilitate the binding of important ions and a decrease in the quantity of superfluous organic materials. There should also be changes in the type of cross-linkages that interconnect the individual parts of the protein. These hypotheses may readily be verified by their implications for systematics; they predict that certain types of correlations will occur between taxonomic groupings, environmental and physiological relationships, and chemical composition.

CHEMICAL METHODS

The shell material was separated mechanically from all extraneous proteins and after being ground to a powder, decalcified, in the presence of 10% trichloracetic acid solution, by hydrochloric acid, added in quantities stoichiometrically necessary to dissolve the calcium carbonate. The organic remains were centrifuged, washed, and hydrolyzed with 6N hydrochloric acid for 22 hours in vacuo. The amino acids were analyzed by automatic ion-exchange chromatography. The method gives reproducible results of better than 1% at the 10^{-8} molar level for identical runs. The overall variation of two identical samples from the same collection site is less than 3%; this figure includes the variation between specimens, and the errors introduced by decalcification, chromatography and data-handling. (For details, see Degens and Spencer, 1966.)

STATISTICAL METHODS

For the comparison of a few forms, visual inspection of the measurements for each amino acid is adequate to place the various

forms in sequences corresponding to hypothesized evolutionary lineages. With larger samples, however, the task of comparison is facilitated by statistical techniques using a computer. As certain amino acids tend to show a constant ratio relative to each other, they may be combined for the purpose of comparison. By means of a factor analysis, it was possible to reduce the data to a set of factor scores (8 in gastropods, 9 in bivalves), which explain 90% of the variance in the data. The factor scores may then be compared independently, or in an 8 or 9-dimensional hyperspace. We found that separate factor analyses for gastropods and bivalves were desirable, as with increasing phylogenetic diversity the various amino acids show slightly different patterns in their tendencies to vary in correlation with others. Our attempt to combine all the data for the phylum did little more than increase the number of extraneous relationships.

The statistical methods used here should not be confused with what has been called "numerical phenetics." Factor analysis, which has become the method of choice in psychology, but which has found little use in systematics, has several advantages over the clustering techniques employed, for example, by Sokal and Sneath (1963). A clustering technique tells nothing more than how "similar" things are, in terms of an arbitrary standard; what is called "overall similarity" is merely the summation of diverse properties which may be no more comparable than the shape and hardness of lightbulbs and pears. It is advantageous, when using any type of statistical technique, to work with a clearly formulated model. A factor analysis generates such a model, allowing the treatment of each individual factor as independent evidence, and its separate evaluation. It also enables one to formulate hypotheses and test them by reference to particular aspects of the data.

At first we tried to relate the species by considering each species as a point within the 8 or 9-dimensional factor space. The factor scores are the coordinates of the points. Species that have similar scores will be separated by only a short distance, while those with greatly different scores will be well separated. Table 1 presents the linear distances between each of the species in the factor space. This kind of comparison, although suggestive of relationships, was ambiguous and misleading. It only told how "similar" the material was, in terms of the new factors. On the basis of other evidence, it was obvious that certain clearly unrelated forms were grouped close together. This is readily understood, for the different amino acid variations are not strictly commeasurable, and

the values give only sequences. That is, the ordering is an intensive, not an extensive one (Ghiselin, 1966a). It is not surprising, therefore, that the summation of similarities grouped together: 1) unrelated forms which had changed little from the ancestral state; 2) unrelated forms which had undergone the same change to an extreme degree; and 3) "advanced" forms which had attained the same grade through parallelism.

Yet by taking the series of factor scores as independent evidence, and arranging the species in series which show changes for each factor in a particular *direction,* it was possible to arrange the various forms in series corresponding to divergent genealogical lineages. The forms previously misplaced then fell into more reasonable positions, and it could be demonstrated that the earlier misplacement had been due, say, to great alteration, in diverse lineages, of one particular factor. It was possible to verify these inferred relationships by means of comparative anatomical evidence. Our data are here presented (Tables 3 and 4) in the form of series showing progressive changes in factor scores. The series correspond to a system of inferred phylogenetic relationships, diagrammed as a phylogenetic tree shown on the left, with the direction of trends shown by arrows. The phylogenetic trees are strictly genealogical; distances mean nothing. The diagrammed arrangements are those which are most strongly supported by our amino acid evidence, and reasonably consistent with comparative anatomy. As a number of alternative interpretations are possible, the reader may wish to evaluate them. This can easily be done by writing out the factor scores on paper, and cutting out strips giving the scores; these may then be placed in any desired sequence.

SYSTEMATIC METHODS

Although we have stressed supra-generic relationships, future work will probably depend on precise species identifications. Therefore we have taken the precaution of figuring (Plates 1, 2) representatives of most of our samples, and have drawn upon materials deposited in the Museum of Comparative Zoology.

Future work may have to incorporate a larger and more rigorously selected sample than does this preliminary study, in order to account for variation. We have selected several specimens from widely separated localities and different ecological conditions, and find that there is considerable temperature-dependent variation (Degens *et al.,* 1966). The particular type of variation that occurs, however, appears to be different for each species. Some

evidence that convergences occur when there is a change from marine to freshwater or terrestrial habitats will be discussed below. The environmental effects can be considered "noise" in evaluating genealogical relationships. If we could remove some of the environmental effects, perhaps some of the anomalous relationships could be resolved. The removal of these effects would require accurate environmental data for each species, selected for a wide range of conditions, and, preferably, experimental studies.

To some extent, this study is based upon traditional comparative anatomical methods. The material studied consists of highly-structured proteins, the parts of which have relational properties such as allow one to abstract a common type from which all may be derived. To be sure, we do not know the details of structure, but our techniques do allow us to infer that different changes have taken place, and to correlate these with each other. However, our argument is not limited to such formal comparison, as our hypothetico-deductive system includes premises about chemistry and evolution which affect the results.

The hypothetical biochemical explanations outlined above imply that there will be a gradual diminution in the quantity of carbohydrate and protein in correlation with evolutionary development. At the same time, there should be a general trend toward increase in chemical groupings useful for nucleation (e.g., aspartic acid) and for cross-linkages (e.g., phenolic compounds). Further, forms which retain a high amount of protein should be those with a structure which may readily serve as a precursor for more modified forms. The primitive condition may therefore be inferred on the basis of physiological criteria, providing independent evidence for inferences based on divergent specialized types. We do not, however, presuppose an overall "primitiveness" for any particular organism. Different structures may evolve at different rates, and the ancestral form of a group may be reconstructed with rigor only when the hypothesized properties of each system are supported by empirical evidence. This point is crucial in the present study, which shows that there is no strict correspondence between the degree of evolutionary advance in the shell and in other structures.

Perhaps the major difficulty for any phylogenetic study is parallelism, and the present study is no exception. Evolutionary changes may tend in the same direction, and occur repeatedly. When this happens, a grouping together of similar forms on the basis of such changes leads to a series of grades rather than clades. It is

abundantly clear in bivalves, for example, that some of the structural changes (in hinges, gills, stomachs, etc.) used as phylogenetic evidence have evolved a number of times. Classifications erected on only one such line of evidence take it as *a priori* that some character can only have evolved once (e.g., Purchon, 1959). Such premises are not only without support, but are flatly contradicted by analogy with such polyphyletic structures as the mammalian ear-bones. If a structure evolves once, it can evolve repeatedly. The problem of parallelism has been de-emphasized by Remane (1956), and Sokal and Sneath (1963), on the grounds that sometimes there is divergence rather than parallelism. This misses the point; there is no way to estimate the probability for a structure to evolve in more than one direction.

A solution to the problem of parallelism has been proposed by Bock (1959, 1960) and has found some application by one of us (Ghiselin, 1966b) in gastropod phylogeny. To understand the technique, one must realize that it entails a shift in emphasis from observed characters to a model of divergent genetic and anatomical potentialities. It is assumed that however many times a character develops, closely related lineages *may* evolve in different directions; this follows from similarities and differences inherent in the genetic potentialities within each lineage. If the forms can be placed in at least two sequences corresponding to divergent tendencies (rather than parallel stages), then the arrangement supports the view that each member of one divergent group is not related to any member of any other such group. From placing them in sequences which do not diverge, but proceed to only one derived state, no systematic inferences can be drawn, as any number of changes would explain the facts; founding groups on lack of divergence in a derived trait is therefore the logical fallacy of denying the antecedent in a conditional statement. In other words, the development of a character is not evidence as such for relationship to a form also having that character, but only that both of the two forms having it are not related, for the same reason, to a form having some different alternative. For example: Purchon (1958, 1959) has distinguished five types of stomachs in bivalves. Three of these occur in the "higher" bivalves studied here: types III, IV and V. Both III and V may be derived from IV, and the advanced types overcome certain functional inefficiencies in the ancestral form. If the bivalves are divided into groups, including one for forms with type V stomachs, and one for those with type III, reference to other kinds of evidence demonstrates that forms within each grouping are most closely related to forms with type

IV. Therefore, the changes from IV to V, and from IV to III have occurred more than once. Nonetheless, a system of relationships which abstracts one group with type IV and only type V, and another with type IV and only type III, fits in quite well with other evidence (cf. Newell, 1965). The biochemical evidence given here likewise supports this division as indicative of relationships. A valid phylogenetic method, then, admits any number of unidirectional changes, as IV to III or IV to V; a contradiction arises only when the divergent, derived forms (III and V) both occur within more than one lineage. Such a shift in emphasis may seem minor, especially when the logic of conditional statements is overlooked, but it seems to resolve much of the confusion that has resulted through efforts to erect systems of classes differentiated by visible, intrinsic properties, rather than corresponding to the more fundamental genetic and evolutionary order. Classification, in other words, involves, not simply grouping organisms on the basis of resemblances, but sorting them out into groups which differ in their programmed genetic information, and therefore have divergent potentialities and tendencies, irrespective of whether these at any moment are realized or not.

PHYLOGENETIC SURVEY

Ancestral models, Amphineura, Cephalopoda, Monoplacophora. By analogy with other studies on protein evolution, one might assume that differences in the matrix protein have resulted from replacement of particular amino acids owing to corresponding chromosome mutations affecting the template. Such modifications may underlie some of the diversity, but we feel that the major reason is to be sought elsewhere. Chemical and electron microscope studies (for references cf. Degens *et al.*, 1966) indicate that the protein is heterogeneous. Solubility tests (Degens and Spencer, 1966) suggest that the protein of *Mercenaria* resembles collagen in solubility and molecular weight, although our quantitative data show differences in amino acid ratios; for example, the molluscan shell matrix differs from its analogue in vertebrate bone, in lacking the hydroxyproline characteristic of collagen.

Some amino sugar is present in both shell and mantle of mollusks. The amount of carbohydrate in the shell varies considerably throughout the phylum. The relative proportion of carbohydrate to protein seems to have decreased progressively with functional improvement in shell structure; simultaneously, the percentage of protein has decreased, but at a different rate. These

trends may be explained if one hypothesizes that the shell was produced from a protein-carbohydrate complex which has been modified so as to improve nucleation. Such a change has occurred in calcified arthropod integuments (Rudall, 1963; Carey *et al.*, MS), which show a decrease in the proportion of protein and an increase in the amount of hexosamine with calcification. In gastropods and bivalves, on the other hand, amino sugars decrease greatly. The integument of arthropods and mollusks may be derived from a common ancestral precursor (presumably originating at an annelidan stage of evolution) in which a non-calcified protein was linked to carbohydrate. In arthropods, the amino sugars have evidently been retained, while protein has been so altered as to expose the acidic and basic side-chains responsible, respectively, for concentrating calcium and carbonate ions. Mollusks differ in having lost much of the amino sugar, while elaborating the protein.

Our data suggest that the molluscan shell has been evolved by modification of proteins which occurred in the mantle. Reference to Table 2 shows the type of relationships and evolutionary changes that seem to characterize the phylum. Here comparisons are given of the amino acid ratios in both mantle and shell of a chiton (*Chaetopleura*), the shells of several cephalopods, representative "primitive" gastropods and pelecypods, a monoplacophoran (*Neopilina*), and the calcified and non-calcified integuments of portunid crabs. The relationships shown by this table are, at first glance, ambiguous. It may be seen that certain amino acids are more (or less) abundant in the shell than in the mantle of *Chaetopleura*. Often, these particular amino acids occur in about the same concentration, as in *Chaetopleura, Spirula* and *Sepia,* whereas in *Loligo, Nautilus* and other mollusks, the range is distinctly different (e.g., aspartic and glutamic acids, perhaps glycine and alanine, and cystine). This relationship is explicable in terms of a high degree of calcification, without loss of carbohydrate, in *Chaetopleura, Spirula* and *Sepia.* Perhaps *Loligo* somewhat resembles *Nautilus* because although it is rich in carbohydrate, it is not highly calcified. In a number of other amino acids, however, *Loligo* is (in correlation with the high ratio of carbohydrate to protein, but independent of calcification) close to *Chaetopleura, Spirula* and *Sepia,* and most distinct from *Nautilus, Haliotis, Nucula* and *Mytilus* (threonine, proline, perhaps glycine and alanine, valine, methionine, isoleucine, leucine, tyrosine, phenylalanine and perhaps hydroxylysine). Of these, only four (threonine, methionine, tyrosine and phenylalanine) would seem to correlate with

the high level of carbohydrate in *Chaetopleura, Spirula, Sepia* and *Loligo*. Any attempt to give phylogenetic interpretations to these relationships without weighting would be foredoomed to failure. *Nautilus,* which retains many primitive traits, more closely resembles members of other classes than its closest relatives. The only cephalopod much like it is *Loligo*. But *Loligo* is, in a way, intermediate between *Nautilus* and the other cephalopods in just those characters in which the latter resemble the Amphineura. There must have been convergences.

The ambiguity may be resolved if one supposes that there have been three, largely parallel, stages in the evolution of the shell. *First,* there would be the development of a calcified, but carbohydrate-rich shell. *Chaetopleura, Spirula* and *Sepia* would represent this stage. *Loligo* would retain much of the character of the first stage, but have lost (or conceivably never have developed) some of the functional units related to calcification, while retaining others significant in carbohydrate physiology. *Second,* there would be a loss of carbohydrate. This would explain the difference between *Nautilus* and other cephalopods, and, as a convergence, the resemblances between *Nautilus* and *Haliotis,* etc. *Third,* there would be an elimination of that part of the protein which is superfluous as a structural element or in calcification, and the development of more efficient means of cross-linkage. These three stages would occur more or less in parallel fashion, perhaps simultaneously, but a stepwise sequence would explain such evident gaps as that between *Nautilus* and other cephalopods.

Within the Cephalopoda, the shell of *Nautilus* is the most advanced in its chemical evolution, in sharp contrast to its many primitive anatomical features. The other cephalopods would appear to have survived in spite of a poorly-developed shell, largely by converting it to an endoskeleton. The *Chaetopleura* shell is of equally low chemical grade; there is no reason to think that this has occurred by degeneration. *Neopilina* belongs to the class Monoplacophora, thought to be ancestral to many other classes of mollusks, but it does not show any close agreement in amino acid ratios to any other mollusk. However, as we were unable to separate all the periostracum from our sample, the data are hard to interpret. On the other hand, the proportions of carbohydrate, protein and mineral show that the shell of *Neopilina* has undergone considerable modification.

It appears that the major, early steps in shell evolution (calcification, loss of carbohydrate) are parallel and unidirectional. Therefore, while of physiological interest, they are uninformative for

cladal phylogeny. In later stages, however, many divergences occur, and these are most useful in establishing genealogical relationships. Such changes may be largely due to different kinds of cross-linkages. These are primarily covalent linkages, such as: 1) various linkages to carbohydrate moieties; 2) disulfide connections; 3) unusual amino acids (e.g., desmosine and isodesmosine); 4) phenolic compounds and quinones (for details, see Degens *et al.,* 1966). The matrix seems to be secreted as soluble precursors which, at about the time of secretion, are acted upon by enzymes and other substances which produce the cross-linkages. Differences in composition may result from variations in the rates and kinds of such processes of secretion and modification, as well as from differences in the raw materials. The subsequent discussions of gastropod and bivalve shell evolution trace out progressive changes in various groups; these changes evidently are related to different kinds of secretory processes and materials.

Gastropoda. Table 2 shows the raw data for *Haliotis,* a form which approximates a hypothetical ancestral gastropod. Changes within the class are shown in Table 3. As would be expected from the usual classification of the order Archaeogastropoda, *Haliotis* (superfamily Zeugobranchia) and *Astraea* (superfamily Trochacea) are quite similar. But *Fissurella,* another zeugobranch, is quite distinct from *Haliotis;* as it shows no clear relationship to any other group, the difference is probably due to divergence. The superfamily Patellacea, as shown by *Acmaea,* is likewise distinct and isolated. The representative of the other archaeogastropod superfamily, Neritacea (*Nerita*), resembles *Viviparus,* a form usually placed in the order Mesogastropoda. Both *Nerita* and *Viviparus* are in some ways transitional between the Archaeogastropoda and Mesogastropoda; the resemblance may be convergent, but there is no compelling reason to think that it is.

The rest of the gastropods studied break down into three major groupings which agree fairly well with generally recognized natural groups. The less-modified members of each group are quite similar, indicating a close relationship and common origin.

The first of these groups (Table 3, *Crepidula* to *Murex*) includes the order Neogastropoda as a distinct sub-group and most of the Mesogastropoda (excepting only some forms known to have opisthobranch affinities). The Neogastropoda (*Colus, Nassarius, Urosalpinx* and *Murex*) show distinctive tendencies in the modification of several factors, although the original pattern is not far removed from that of mesogastropods. This fits in with other biological data; the neogastropods are distinct but not greatly

modified in terms of morphology, except for the more specialized members of the group. But neogastropods are distinct in chromosome number (Nishikawa, 1962) and evidently in many physiological characters also. The superfamily Naticacea (here, *Lunatia* and *Polinices*) has a pattern of change clearly distinct from other mesogastropods, and proceeding in a direction opposite to that of, say, *Littorina* and *Cypraea*. One of the unexpected results of this study was that *Melanella* has the same tendencies as occur in the Naticacea. *Melanella* has been placed in the superfamily Aglossa, which may be an artificial assemblage of parasitic forms with tall shells. An affinity of *Melanella* to the Pyramidellidae (now grouped as opisthobranchs), as suggested by Thiele (1935), is not consistent with our findings; similarly, *Melanella* lacks the characteristic reproductive system and larval shell of opisthobranchs.

Littorina, which, along with other members of the superfamily Littorinacea, is often thought to stand near the base of the mesogastropod series, has a pattern of change which tends in the direction characteristic of *Cypraea* and *Crepidula,* fitting in well with the concepts of Thiele (1935). An affinity between the Cypraeacea (*Cypraea*) and Calyptraeacea (*Crepidula*) follows from intermediate forms (Lamellariacea) (cf. Fretter and Graham, 1962). The type of variation that occurs within a genus may be seen in *Crepidula.* The range is fairly narrow and in conformity with overall trends, but some of the factors appear to have changed more than others. Such variation clearly indicates that a larger sample will be necessary in future work, but the utility of the method stands.

Another distinct grouping of mesogastropods consists of *Turritella* (Cerithiacea) and *Epitonium* and *Janthina* (Ptenoglossa). Both superfamilies differ from all other gastropods in possessing a curious, spermatophore-like structure, the spermatozeugma. The Cerithiacea are of disputed taxonomic position, often looked upon as transitional between various major lineages of mesogastropods and opisthobranchs; our data suggest a closer affinity to opisthobranchs. However, Cerithiacea and Ptenoglossa also have much in common with Neogastropoda, and the basal members of each of our three main groupings (*Architectonica, Turritella, Littorina,* etc.) are quite similar. Therefore, the precise cladistic relationships of each group remain uncertain.

The third group corresponds to the Euthyneura, or the subclasses Pulmonata and Opisthobranchia. The Euthyneura are characterized by hermaphroditism, a tendency to loss of the effects of

torsion, a distinctive type of spermatozoon, a peculiar ctenidium, and a heterostrophic larval shell (except where secondarily modified). Fretter and Graham (1949) have placed the family Pyramidellidae in this group. As *Architectonica* has a heterostrophic larval shell, Robertson (1963; also, Robertson and Merrill, 1963) and others have argued for its close affinity to the Euthyneura, and this placement is adopted here.

Some workers have advocated abandonment of the subclasses Pulmonata and Opisthobranchia (cf. Taylor and Sohl, 1962). However, this has been done solely on the basis of highly speculative assertions that Pulmonata is a polyphyletic assemblage; there is no real evidence for this view (cf. Ghiselin, 1965, 1965b).

In its low protein content, and in the amino-acid ratios, *Architectonica* is an excellent precursor for the opisthobranchs and pulmonates, the members of each of which can readily be derived by modification of different factors. This fits in with the larval shell types. Chemically, *Architectonica* differs but slightly from such Cerithiacea as *Turritella.* Indeed, Thiele (1929) put *Architectonica* in the Cerithiacea. On the basis of fossil evidence, Knight, Batten and Yochelson (1954) relate the superfamily Ptenoglossa to the Pyramidellidae and group both with the opisthobranchs. Clench and Turner (1951) likewise stress the opisthobranch affinities of Ptenoglossa. Thus the close relationships between these groups, on the basis of other evidence, supports the inference from shell biochemistry.

The general conclusions reached by one of us on the basis of various lines of evidence on the relationships of opisthobranchs (Ghiselin, 1966b) are fairly well borne out by the present study. *Bulla* shows a beginning in the development of trends characteristic of the Anaspidea (*Akera, Aplysia*); gizzard morphology and anatomy generally support this relationship. Both *Akera* and *Oxynoe* are distinguished from all other mollusks by the presence of hydroxyproline in the shell. This amino acid is distinctive of collagen; its adaptive advantage is probably one of making the shell flexible, and the same explanation suffices for the rather high protein content. Perrier and Fischer (1911) describe a muscle inserted near the rim of the shell in *Akera* which bends the shell and closes the mantle cavity. An evidently homologous muscle provides a respiratory current in *Cylindrobulla,* a form transitional between Anaspidea and Sacoglossa (including *Oxynoe*) (cf. Marcus and Marcus, 1956); from it may be derived the shell adductor muscle in the bivalved gastropod (Baba, 1961). These homologies,

both morphological and chemical, strongly support the relationship previously inferred (Ghiselin, 1966b) on the basis of reproductive anatomy and spermatozoon morphology. Although both *Aplysia* and *Dolabella* are universally looked upon as closely related to *Akera,* neither contains hydroxyproline in its shell. *Aplysia* is closest to *Akera,* but deviant, and *Dolabella* is so distinct that no particular relationship for it follows from our data. Although Table 3 shows *Akera* and *Oxynoe* more closely related to each other than to *Aplysia,* which is a possibility, it seems more reasonable to infer that *Aplysia* and *Dolabella* have lost their former resemblances to *Akera;* their shells are vestigial and no longer function in the adults. *Cavolina* (order Thecosomata) and *Umbraculum* (order Notaspidea) are here grouped together on the basis of a few similarities, especially factor 4; however, to place *Cavolina* with the *Akera-Bulla* group, as previously suggested on the basis of admittedly weak anatomical evidence (Ghiselin, 1966b), would be fairly consistent with our data.

Insufficient information was available to establish relationships for the basommatophorous Pulmonata (*Siphonaria, Helisoma* and *Planorbis*), beyond relating them to other Euthyneura. In the Stylommatophora, on the other hand, the relationships seem clear: *Achatinella* (suborder Orthurethra) and *Succinea* (suborder Heterurethra) are very close. Admitting the possibility of convergence due to a terrestrial habitat, our data contradict the view of Rigby (1965) that *Succinea* is an opisthobranch with affinities to the Anaspidea (*Akera, Aplysia,* and *Dolabella*). The pulmonate nature of *Succinea* is further supported by its stylommatophoran chromosome morphology (Inaba, 1959), gizzard type, nervous system, and reproductive morphology and cytology.

Bivalvia. The relationships of bivalves have long been controversial, owing to parallelism, convergence, and an insufficient number and variety of characters. (For a useful summary of the data which have been used, see Newell, 1965.) Hinge-teeth (Dall, 1894, and others) have been very useful, especially with fossils, and are particularly useful in that some types are divergent, but some convergences have taken place. The attempts of Pelseneer (e.g., 1911) to divide the bivalves on the basis of gill elaboration result in partially artificial groupings, because of unidirectional, parallel evolution. There are analogous difficulties with palp types (Stasek, 1963), kidneys (Odhner, 1912) and the pallial sinus. Douvillé's (1912) division into normal, sedentary and burrowing branches does show fair correspondence to other groupings, and this is to

be expected, as the branches are divergent. Again, certain specializations for which there seems to be no unidirectional trend give groupings which correlate with other types of evidence: certain types of cilia on the gill (Atkins, 1938), and the anisomyarian state. We have already alluded to the value of some modified and divergent stomach types (Purchon, 1958, 1959). When the available evidence is properly weighted — emphasizing divergences and recognizing possible effects of parallelism and convergence — the bivalves fall quite readily into natural groupings which may be supported on the basis of various kinds of evidence. The same is true of the new information summarized here. Although the precise sequence of genealogical relationships remains uncertain, the general pattern obtained correlates quite rigorously with other types of evidence. Indeed, our groupings correspond almost perfectly with the classification proposed by Newell (1965), except that our data (and some other evidence) suggest removing one group to another, closely related one.

Our data are presented as factor scores in Table 4. *Nucula* may be considered as having properties closest to the common ancestor of the class. We give no starting point for the tree because the data are consistent with a variety of interpretations, although the common stem presumably is near to *Nucula*.

Nucula, Solemya, Malletia and *Yoldia* are members of the order Protobranchia, a group generally held to be representative of the ancestral bivalve stock. The placement of *Malletia* and *Yoldia* close together, distinct from *Nucula* is in agreement with the usual classifications (McAlester, 1964). *Solemya* is similar to *Nucula* but somewhat modified, and its relationship to the Nuculanidae (*Malletia, Yoldia*) is only weakly supported by our data. Newell's (1965) removal of *Solemya* to a taxon of rank equal to that of other protobranchs is perhaps based on an overemphasis of shell morphology.

Periploma and *Lyonsia* are not greatly altered from the *Nucula* stage. The pattern of modification agrees well with their usual classification as Pandoracea, and with the view that they are but distantly related to the other major groups of higher bivalves included in this study. *Neotrigonia* is of uncertain relationship. The position shown is only weakly supported by our evidence. Indeed, it would in many ways be more satisfactory to relate it to the Arcidae (*Anadara* and *Limopsis*) as suggested by Odhner (1912) and others. It shows a pattern of change which is intermediate between *Mytilus* and *Anadara* in factors 3, 4, 5, and 9; only factor 1 is out of place, and this could be a divergent or ancestral state.

The connections shown on the diagram for *Anadara* and *Limopsis* serve only to suggest a possible relationship of other bivalves to one lineage: the two genera are closely related. A close relationship of the Arcidae to the Anisomyaria (*Mytilus, Crassostrea* and *Aequipecten*) is supported by the presence, in the Arcidae, of micro-laterofrontal cilia, which are common in Anisomyaria (Atkins, 1938), and also by the type III stomach (Purchon, 1957) which occurs only in Pteriomorpha (*Mytilus* and *Crassostrea,* but not *Aequipecten*).

The remaining bivalves are Heterodonta (*sensu* Newell, 1965). *Pitar, Mercenaria, Saxidomus* and *Petricola* are all members of the Veneracea, and clearly form a natural group, as do *Corbicula* and *Arctica* (Corbiculacea). The placement of *Macoma* and *Tagelus* (Tellinacea) with *Mulinia* and *Laevicardium* is in agreement with Newell's (1965) classification, but inclusion of the Corbiculacea in this grouping is not. However, *Mulinia* and some of its allies share with the Corbiculacea a desmodont hinge, unlike the Veneracea; the hinge of the Tellinacea is likewise aberrant, although *Laevicardium* (here placed as an early offshoot of the Tellinacea-Corbiculacea line) is heterodont.

NOTES ON ECOLOGY

Invasion of land and fresh water. In the present study we have, on the whole, attempted to hold the environment constant by selecting our material from similar habitats. An exception is a few freshwater and terrestrial forms. The effects of such a drastic change in habitat are striking. In Table 5 are compared two fairly closely related prosobranchs, the marine *Nerita* and freshwater *Viviparus,* and a similar series of two marine Euthyneura (*Architectonica* and *Siphonaria*), two freshwater pulmonates (*Helisoma* and *Planorbis*) and two land pulmonates (*Succinea* and *Achatinella*). In general, the same amino acids change in the same direction with shifts to both land and fresh water: aspartic acid (factor 8); threonine, glutamic acid, glycine, methionine (factor 1); perhaps histidine (factor 3); proline, arginine (factor 4); serine, alanine, phenylalanine (factor 6). It holds true as a general rule, that the change in concentration for these amino acids is in the direction of the concentrations that prevail in more primitive mollusks such as *Haliotis* and *Nucula* (Table 2). Other amino acids either remain constant or change in the opposite direction in terrestrial forms: valine, isoleucine and leucine, i.e., factor 2. Tyrosine (factor 3) seems to change in the direction away from

the primitive state; the freshwater forms change to a greater degree than the terrestrial ones. The other members of factor 3 (hydroxylysine, lysine and histidine) show no clear-cut pattern, but tend to approach the primitive level. Tyrosine and phenylalanine seem anomalous, but this may be due to their both being phenolics. Although we do not have enough data to obtain conclusive results (especially since we do not have several lineages of terrestrial forms), the evidence suggests that convergent changes occur in freshwater and terrestrial environments. It is probable that the shift to a new habitat makes it advantageous to concentrate the same functional units which had been decreased, in proportion, among advanced marine forms. Such a pattern of change is consistent with the presumed heterogeneity of the protein. When the structure and function of the substances underlying the variation are known, it should be possible to explain just why particular changes take place.

Effects of salinity and temperature. The sample given here is large enough only to be suggestive, but there is reason to think that within a species, salinity and temperature may have some effect on amino acid ratios. However, the effect seems to be characteristic for each species, and there is little evidence that particular amino acids vary consistently in correlation with salinity or temperature for larger taxa as a whole. Hare (1962) measured the amino acid content for *Mytilus californianus* over a wide range of temperatures, and found no correlated change in protein composition. Comparison of other species (*M. edulis* and *M. viridis*) from widely different habitats supports the same view (Degens and Spencer, 1966). However, the periostracum of *Tagelus divisus* is distinctly different in forms from Bermuda, on the one hand, and Nantucket and Long Island, on the other (Degens *et al.*, 1966). A factor analysis of the shell matrix proteins in *Polinices duplicatus, Mulinia lateralis* and *Anadara transversa* (Degens *et al.*, 1966) shows that there is a distinct correlation between mean temperature and salinity and certain of the factors used in establishing genealogical relationships. *Mulinia* and *Anadara* both showed the same direction of change in factors 1 and 5, but only *Mulinia* changed progressively in factor 8, while *Anadara* changed in factors 2, 6 and 9. *Polinices* changed in the opposite direction in the threonine-glutamic acid-glycine factor. For *Mulinia,* a multiple regression analysis was run to evaluate the degree of predictibility of each amino acid from the following environmental parameters: median temperature, range of temperature, median salinity, range of salinity, and depth. These analyses showed that only in the case of isoleucine, leucine, valine and cystine, was a statistically significant

linear regression obtained. For example, 82% of the variance of isoleucine is explained in terms of the environmental parameters. Of these, the median temperature and range of salinity were by far the most important, accounting for *ca.* 45% and *ca.* 30% of the variance, respectively. Such temperature dependent variation as occurs may reasonably be attributed to differential effects of temperature on the various chemical processes involved in shell deposition. Some of the patterns of variation may ultimately be related to genetic differences and therefore cast light on the evolution of the underlying physiological mechanisms. The precise significance of such variation must await the accumulation of a sufficient body of relevant data, but the problem is under investigation.

CONCLUSIONS

Success in grouping mollusks on the basis of shell matrix proteins suggests that the method may prove useful in the future. However, the precise placements given by this study must remain speculative until more adequate samples and better techniques are available for dealing with ecological variation and other problems. Preliminary results (Degens *et al.*, 1966) indicate that periostracum also is useful for phylogenetic inference, and other tissues show promise.

In any such study as this, it is essential that rigorous methodology be employed. This is clear-cut evidence that various lineages have undergone the same changes repeatedly and independently. Because of mosaic evolution, the rates at which changes occur in a single lineage are not necessarily the same for different structures. It is both bad biology and fallacious logic to place whole organisms in a series from "primitive" to "advanced" forms and argue that one has a real series of genealogical relationships. The term "primitive" is correctly used in a descriptive sense, in referring to the earlier stages of an evolutionary sequence. In such comparisons it is perfectly valid to assert, for example, that the noncalcified molluscan shell is more primitive than the calcified. But such comparisons give only intensive sequences: it is nonsense to measure "primitiveness" by summing up the degree of advancement in several different systems, as the various comparisons are not in commeasurable units. The present study illustrates this point very well. In terms of the degree to which metamerism has been lost, one could rank some mollusks thus: *Neopilina; Nautilus; Chaetopleura; Sepia; Haliotis* and *Nucula.* In terms of eye anagenesis, the

order would be: *Neopilina* (?); *Chaetopleura* and *Nucula; Haliotis; Nautilus; Sepia.* For shells it would be: *Chaetopleura* and *Sepia; Nautilus, Haliotis* and *Nucula; Neopilina.* The absurdity of trying to elaborate a calculus of evolutionary advance should be obvious. Nonetheless, one often reads assertions that a particular relationship should be rejected because modern members of some group are not "primitive" enough for some of their characters to represent the ancestral state. The present confusion in molluscan taxonomy may be expected to continue as long as such fallacy is perpetuated.

The approach has obvious use in developing a comparative biochemistry and physiology of calcification. The matrix is sometimes preserved in fossils, and study of its paleontology has already begun (Degens and Love, 1965; Degens and Schmidt, 1966). The effects of environmental factors should be particularly interesting. A change to fresh water from the sea would affect the pH and various ion concentrations, as is suggested by the rather high protein levels in freshwater forms. Where the calcification mechanism is inefficient, and where the medium in which calcification occurs is not regulated, slight changes in the environment — ionic ratios, pH, temperature, etc. — might have great effect on biota. Conceivably, physical and chemical changes in the environment might help to explain the greater abundance of fossils in Cambrian and younger rocks than in older ones, and mass extinction of ammonites and nautiloids. It is well known that the formation of coral reefs is dependent on temperature, and it seems a reasonable analogy that the success or failure of many organisms may be intimately connected with the process of calcification.

SUMMARY

1. Measurements of the amino acids in the shells of selected mollusks show a wide diversity. Some differences may be related to progressive evolutionary development of the shell.

2. Factor analysis shows that 90% of the variance may be explained in terms of a few factors. A technique which overcomes problems of parallelism and convergence has been developed for inferring phylogenies on the basis of differences in the factor structure.

3. Various phylogenetic hypotheses and classification schemes are evaluated on the basis of the evidence obtained in the study. The results are in close agreement with conventional classification systems, and cast some light on the positions of forms of disputed relationship.

4. Preliminary results show that there are convergences with shifts from marine to freshwater habitats, and that temperature and salinity dependent variation poses a considerable, but not insoluble, problem of interpretation.

REFERENCES CITED

ATKINS, D.

1938. On the ciliary mechanisms and interrelationships of lamellibranchs. Part VII, latero-frontal cilia of the gill filaments and their phylogenetic value. Quart. J. Microscop. Sci., **80**: 345-436.

BABA, K.

1961. On the identification and the affinity of *Tamanovalva limax*, a bivalved sacoglossan mollusc in Japan. Publ. Seto Mar. Biol. Lab., **9**: 37-62.

BOCK, W. J.

1959. Preadaptation and multiple evolutionary pathways. Evolution, **13**: 194-211.

———.

1960. The palatine process of the premaxilla in the Passeres. Bull. Mus. Comp. Zool., **122**: 361-488.

BØGGILD, O. B.

1930. The shell structure of the mollusks. Kgl. Danske Videnskab. Selskabs, Skr. Naturvidenskab. Math. Afdel., (9)**2**: 232-325.

BROWN, C. H.

1952. Some structural proteins of *Mytilus edulis*. Quart. J. Microscop. Sci., **93**: 487-502.

CAIN, A. J. (ed.)

1959. Function and taxonomic importance. Systematics Association, London: 140 pp.

CAREY, F. G., D. W. SPENCER and E. T. DEGENS

MS Amino acids and amino sugars in calcified tissues of portunid crabs. (MS in preparation.)

CLENCH, W. J. and R. D. TURNER

1951. The genus *Epitonium* in the Western Atlantic, Part I. Johnsonia, **2**: 249-288.

DALL, W. H.

1894. Contributions to the Tertiary fauna of Florida. Part III, a new classification of the Pelecypoda. Trans. Wagner Free Inst. Sci., **3**: 485-570.

DEGENS, E. T., and S. LOVE

1965. Comparative studies of amino acids in shell structure of *Gyraulus trochiformis* Stahl, from the Tertiary of Steinheim, Germany. Nature, **205**: 876-878.

———, and H. Schmidt
1966. Die Paläobiochemie, ein neues Arbeitsgebiet der Evolutionsforschung. Paläontol. Zeitschr., **40** (in press).
———, and D. W. Spencer
1966. Data file on amino acid distribution in calcified and uncalcified tissues of shell-forming organisms. Technical Report. Woods Hole Oceanographic Institution, Reference No. 66-27.
———, ——— and R. H. Parker
1967. Paleobiochemistry of molluscan shell proteins. Comp. Biochem. Physiol. **20**: 553-579. (In press.)
Douvillé, H.
1912. Classification des lamellibranches. Bull. Soc. Géol. France, (4)**12**: 419-467.
Fretter, V. and A. Graham
1949. The structure and mode of life of the Pyramidellidae, parasitic opisthobranchs. J. Mar. Biol. Assoc., U. K., **23**: 493-532.
———
1962. British prosobranch molluscs. Ray Society, London. xvi + 755 pp.
Ghiselin, M. T.
1965. Is Pulmonata a monophyletic taxon? Ann. Rep. Amer. Malacological Union, 1965: 19-20.
———
1966a. On psychologism in the logic of taxonomic controversies. Systematic Zool., **15**: 207-215.
———
1966b. Reproductive function and the phylogeny of opisthobranch gastropods. Malacologia, **3**: 327-378.
Glimcher, M. J.
1960. Specificity of the molecular structure of organic matrices in mineralization. *In* R. F. Sognnaes (ed.), Calcification in biological systems. Amer. Assoc. Adv. Sci. Publ. **64**: 421-487.
Gregoire, C.
1961. Structure of the conchiolin cases of the prisms in *Mytilus edulis* Linné. J. Biophys. Biochem. Cytol., **9**: 395-400.
Hare, P. E.
1962. The amino acid composition of the organic matrix of some recent and fossil shells of some west coast species of *Mytilus*. Doctoral thesis, California Institute of Technology.
Inaba, A.
1959. Cytological studies in molluscs. II. A chromosome survey in the stylommatophoric Pulmonata. J. Sci. Hiroshima Univ. (Bl)**18**: 71-93.
Knight, J. B., R. L. Batten and E. L. Yochelson
1954. Status of invertebrate paleontology, 1953. V. Mollusca: Gastropoda. Bull. Mus. Comp. Zool., **112**: 173-179.

Marcus, E., and E. Marcus
1956. On the tectibranch gastropod *Cylindrobulla*. Acad. Brasil. Ci. An., **28**: 119-128.
Margoliash, G., and E. L. Smith
1964. Structural and functional aspects of cytochrome c in relation to evolution. Internat. Congr. Biochem., 6th, New York: 206-207.
McAlester, A. L.
1964. Preliminary suggestions for a classification of nuculoid bivalves. J. Paleont. **38**: 397-400.
Newell, N. D.
1965. Classification of the Bivalvia. Amer. Mus. Novit., No. **2206**: 1-25.
Nishikawa, S.
1962. A comparative study of the chromosomes in marine gastropods, with some remarks on cytotaxonomy and phylogeny. J. Shimonoseki Coll. Fish., **11**: 149-186.
Odhner N. Hj.
1912. Morphologische und phylogenetische Untersuchungen über die Nephridien der Lamellibranchien. Z. Wiss. Zool., **100**: 287-391.
Pelseneer, P.
1911. Les Lamellibranches de l'expédition du Siboga, partie anatomique. Siboga Expéditie, Monogr. 53a: 125 pp.
Perrier, R., and H. Fischer
1911. Recherches anatomiques et histologiques sur la cavité palléale et ses dépendences chez les Bulléens. Ann. Sci. Nat., Zool., (9)**14**: 1-190.
Purchon, R. D.
1957. The stomach in the Filibranchia and Pseudolamellibranchia. Proc. Zool. Soc. London, **129**: 27-60.
1958. Phylogeny in the Lamellibranchia. Proc. Centenary Bicen. Congr. Biol. Singapore, 1958: 69-82.
1959. Phylogenetic classification of the Lamellibranchia, with special reference to the Protobranchia. Proc. Malacol. Soc. London, **33**: 224-230.
Remane, A.
1956. Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik. 2 ed., Geest and Portig, Leipzig: 364 pp.
Rigby, J. E.
1965. *Succinea putris:* a terrestrial opisthobranch mollusc. Proc. Zool. Soc. London, **144**: 445-486.
Robertson, R.
1963. The hyperstrophic larval shells of the Architectonicidae. Ann. Rep. Amer. Malacol. Union, 1963: 11-12.
——— and A. S. Merrill
1963. Abnormal dextral-hyperstrophy of post-larval *Heliacus* (Gastropoda: Architectonidae). Veliger, **6**: 76-79.

RUDALL, K. M.
1963. The chitin/protein complexes of insect cuticles. Advances Insect Physiol., **1**: 257-313.
SOKAL, R. R. and P. H. A. SNEATH
1963. Principles of numerical taxonomy. Freeman, San Francisco: xvi + 359 pp.
SPENCER, W. P.
1949. Gene homologies and the mutants of *Drosophila hydei*. *In:* G. L. Jepsen, G. G. Simpson and E. Mayr (eds.), Genetics, paleontology and evolution. University Press, Princeton, Ch. **3**: xiv + 474 pp.
STASEK, C. R.
1963. Synopsis and discussion of the association of ctenidia and labial palps in the bivalved Mollusca. Veliger, **6**: 91-97.
TAYLOR, D. W. and N. F. SOHL
1962. An outline of gastropod classification. Malacologia, **1**: 7-32.
THIELE, J.
1929- Handbuch der systematischen Weichtierkunde. Gustav Fischer,
1935. Jena. 2 vols.
WILBUR, K. M.
1964. Shell formation and regeneration. *In:* K. M. Wilbur and C. M. Yonge (eds.), Physiology of Mollusca. Academic press, New York, Ch. 8: xiii + 473 pp.

(Received 13 September, 1966.)

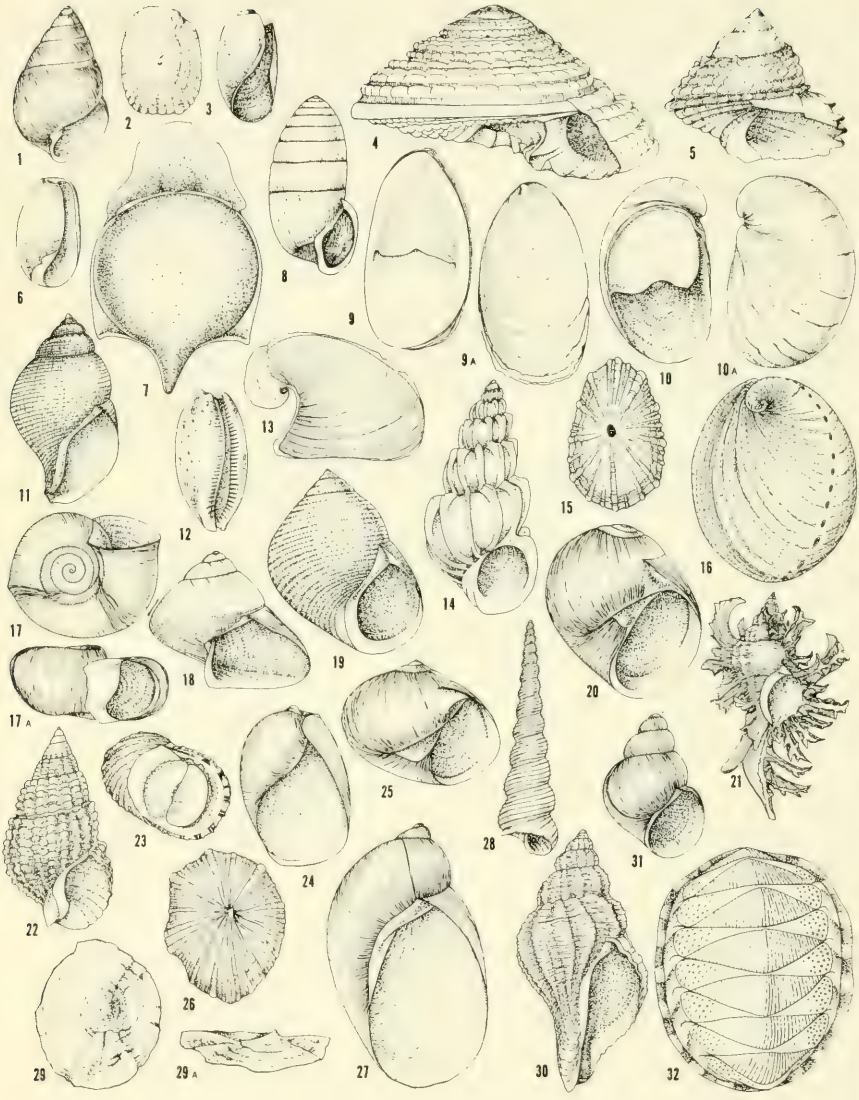
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PLATE I

GASTROPODA

Figure 1. *Achatinella lorata* Pfeiffer, 1848, Oahu, Hawaiian Islands, Pease collection, MCZ (Mollusk Department) — aperture view. X 1.

Figure 2. *Acmaea pustulata* (Helbling, 1799), Puerto Sosya, Dominican Republic, MCZ, coll. 1937 — top view. X 2/3.

Figure 3. *Akera soluta* (Gmelin, 1791), Zanzibar, MCZ No. 4444 — aperture view. X 1/3.

Figure 4. *Architectonica nobilis* (Roding, 1798), Middle Atlantic Coast, 2-10 m, MCZ No. 90867 — aperture view. X 2.

Figure 5. *Astraea caelata* (Gmelin, 1798), Pelican Shoals, Florida, MCZ, coll. 1939 — aperture view. X 2/3.

Figure 6. *Bulla striata* (Bruguiere, 1792), Puerto Vieja, Dominican Republic, MCZ, coll. R. H. Parker, April 1965 — aperture view. X 2/3.

Figure 7. *Cavolina tridentata* (Forskal, 1776), pelagic, West Indies, Alexander Agassiz coll. 1879, MCZ (uncat.) — aperture view. X 2.

Figure 8. *Cerion regium* (Benson, 1849), northeast end of Castle Island, Crooked Island Group, Bahamas, B.W.I. — coll. Robertson and Scott, 1958, MCZ (uncat.) — aperture view. X 2/3.

Figure 9. *Crepidula fornicata* (Linné, 1767), Hadley Harbor, Elizabeth Islands, Massachusetts, Sta. P-2211-65, Systematics-Ecology Program, Marine Biological Laboratory — interior view; 9A, exterior view, X 1 1/3.

Figure 10. *Crepidula plana* (Say, 1822), Hadley Harbor, Elizabeth Islands, Massachusetts, Sta. P-275-65, Systematics-Ecology Program, Marine Biological Laboratory — interior view; 10B, exterior view. X 2/3.

Figure 11. *Colus trophius* (Dall, 1919), off San Francisco, California, 1874-1929 m, coll. R. H. Parker, MCZ (uncat.) — aperture view. X 1 1/3.

Figure 12. *Cypraea zebra* (Linné, 1758), Miami, Florida, MCZ (uncat.) — aperture view. X 1/3.

Figure 13. *Dolabella callosa* (Lamarck, 1801) = *scapula* (Martyn), Calapan, Mindoro, Philippine Islands, MCZ No. 96107 — side view. X 2/3.

Figure 14. *Epitonium angulatum* (Say, 1831), near mouth of New Brazos River, Freeport, Texas, MCZ No. 230893 — aperture view. X 2.

Figure 15. *Fissurella barbadensis* (Gmelin, 1791), Romey Point, Bonnguen Air Force Base, Puerto Rico, MCZ No. 1956 — top view (exterior). X 2/3.

PLATE I (Continued)

Figure 16. *Haliotis cracherodi* (Leach, 1814), San Diego, California, MCZ No. 58659 — exterior view. X 1/3.

Figure 17. *Helisoma trivalvis* (Say, 1817), La Porte, Indiana, MCZ No. 63234 — side view; 17B, aperture view. X 1 1/3.

Figure 18. *Janthina janthina* (Linné, 1767), Cape Florida Key, Biscayne, Florida, MCZ No. 155173 — aperture view. X 5/6.

Figure 19, *Littorina littorea* (Linné, 1758), Hadley Harbor, Elizabeth-Islands, Massachusetts, Sta. P-0610-65, Systematics-Ecology Program, Marine Laboratory — aperture view. X 1.

Figure 20. *Lunatia triseriata* (Say, 1826), Hadley Harbor, Elizabeth Islands, Massachusetts, Sta. P-247-65, Systematics-Ecology Program, Marine Biological Laboratory — aperture view. X 2.

Figure 21. *Murex brevifrons* (Lamarck, 1822), Mayaguez, Puerto Rico, coll. M. R. Carriker, Systematics-Ecology Program, Marine Biological Laboratory — aperture view. X 1/3.

Figure 22. *Nassarius trivittatus* (Say, 1822), Hadley Harbor, Elizabeth Islands, Massachusetts, Sta. P-0605-65, Systematics-Ecology Program, Marine Biological Laboratory – aperture view. X 2.

Figure 23. *Nerita plexa* (Dillwyn, 1817), Mauritius, MCZ No. 139024 — aperture view. X 1/3.

Figure 24. *Oxynoe viridis* (Pease, 1864), from Pease coll., MCZ (uncat.) aperture view. X 2 1/3.

Figure 25. *Polinices duplicatus* (Say, 1822), Provincetown, Massachusetts, MCZ (uncat.) — aperture view. X 1 1/3.

Figure 26. *Siphonaria alternata* (Say, 1826), Bermuda, coll. Bryant, 1903, MCZ No. 24213 — top view (exterior). X 1 1/3.

Figure 27. *Succinea ovalis* (Say, 1817), bank of Grand River, W. Bridge Street Ferry, Ottawa County, Michigan, MCZ No. 166697 — aperture view. X 2.

Figure 28. *Turritella terebra* (Lamarck, 1822), Manila Bay, near Cavite, Luzon, Philippine Islands, MCZ No. 138070—aperture view. X 1/3.

Figure 29. *Umbraculum indicum* (Lamarck, 1819), Hawaii, C. B. Adams coll., MCZ No. 1173 — top view (exterior); 29A, side view. X 1/3.

Figure 30. *Urosalpinx cinerea* (Say, 1822), Hadley Harbor, Elizabeth Islands, Massachusetts, Sta. P-0612-65, Systematics-Ecology Program, Marine Biological Laboratory — aperture view. X 4 2/3.

PLATE I (Continued)

Figure 31. *Viviparus georgianus* (I. Lea, 1834), Lake Woodruff near Fick Island, Volusa County, Florida, MCZ No. 186800 — aperture view. X 2/3.

AMPHINEURA

Figure 32. *Chaetopleura apiculata* (Say, 1830), Hadley Harbor, Elizabeth Islands, Sta. P-7-63, Systematics-Ecology Program, Marine Biological Laboratory — top view (exterior). X 2.

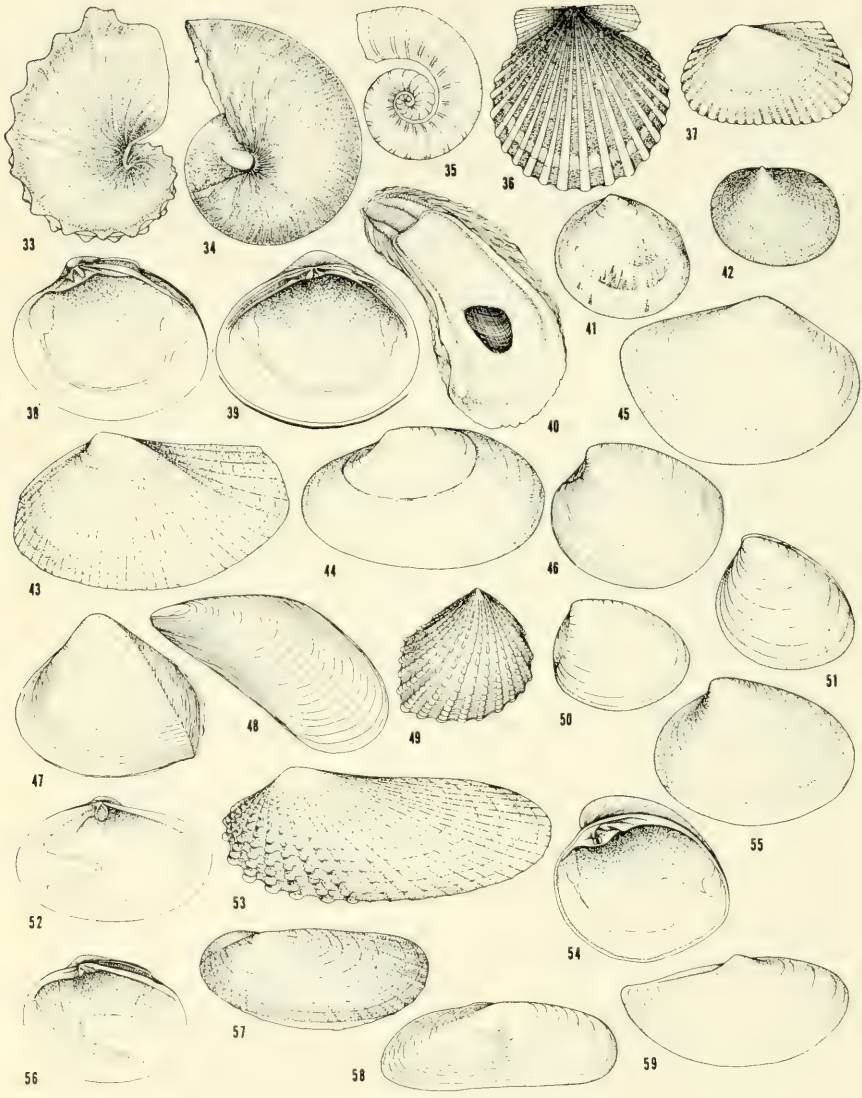
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PLATE II

CEPHALOPODA

Figure 33. *Argonauta hians* (Dillwyn, 1817), southern Tropical Atlantic, MCZ (uncat.) — side view of egg case. X 1/3.

Figure 34. *Nautilus pompilius* (Linné, 1758), Southwest Pacific Ocean, MCZ (uncat.) — side view. X 1/3.

Figure 35. *Spirula spirula* (Linné, 1758), Saint Kitts Island, B.W.I., MCZ (uncat.) — side view. X 1 1/3.

PELECYPODA

Figure 36. *Aequipecten irradians* (Lamarck, 1819), Hadley Harbor, Elizabeth Islands, Massachusetts, Sta. P-65-64, Systematics-Ecology Program, Marine Biological Laboratory — exterior view, right valve. X 1.

Figure 37. *Anadara transversa* (Say, 1822), Hadley Harbor, Elizabeth Islands, Massachusetts, Sta. P-77-64, Systematics-Ecology Program, Marine Biological Laboratory — exterior view, left valve. X 9 1/3.

Figure 38. *Arctica islandica* (Linné, 1758), Georges Bank, Massachusetts, MCZ No. 14325 — interior view, right valve. X 1/3.

Figure 39. *Corbicula consobrina* (Cailliand, 1827), Nile River, Egypt, MCZ No. 14676 — interior view, right valve. X 1 1/3.

Figure 40. *Crassostrea virginica* (Gmelin, 1791), Holding Tank, Supply Department, Marine Biological Laboratory, Woods Hole, Massachusetts — interior view, right valve. X 1/3.

Figure 41. *Laevicardium mortoni* (Conrad, 1831), Hadley Harbor, Elizabeth Islands, Massachusetts, Sta. P-141-64, Systematics-Ecology Program, Marine Biological Laboratory — exterior view, left valve. X 8 1/3.

Figure 42. *Limopsis compressus* (Dall, 1908), off Salina Cruz, Mexico, 1020-1240 m, coll. R. H. Parker, MCZ (uncat.) — exterior view, left valve. X 2/3.

Figure 43. *Lyonsia hyalina* (Conrad, 1831), Hadley Harbor, Elizabeth Islands, Massachusetts, Sta. P-200-64, Systematics-Ecology Program, Marine Biological Laboratory — exterior view, left valve. X 5.

Figure 44. *Macoma tenta* (Say, 1834), Hadley Harbor, Elizabeth Islands, Massachusetts, Sta. P-91-64, Systematics-Ecology Program, Marine Biological Laboratory — exterior view, left valve. X 2 1/3.

Figure 45. *Malletia,* species "M," Atlantic Abyssal Plain, 4970 m, coll. H. L. Sanders, in coll. at Woods Hole Oceanographic Institution — exterior view, left valve. X 2 1/3.

PLATE II (Continued)

Figure 46. *Mercenaria mercenaria* (Linné, 1758), Holding Tank, Supply Department, Marine Biological Laboratory, Woods Hole, Massachusetts — exterior view, left valve. X 2 1/3.

Figure 47. *Mulinia lateralis* (Say, 1822), Hadley Harbor, Elizabeth Islands, Massachusetts, Sta. P-0902-65, Systematics-Ecology Program, Marine Biological Laboratory — exterior view, left valve. X 2 1/3.

Figure 48. *Mytilus edulis* (Linné, 1758), Hadley Harbor, Elizabeth Islands, Massachusetts, Sta. P-148-64, Systematics-Ecology Program, Marine Biological Laboratory — exterior view, left valve. X 2 2/3.

Figure 49. *Neotrigonia margaritacea* (Lamarck, 1803), New South Wales, Australia, from coll. of A. L. McAlester, Yale University — exterior view, right valve. X 2/3.

Figure 50. *Nucula proxima* (Say, 1822), Hadley Harbor, Elizabeth Islands, Massachusetts, Sta. P-92-64, Systematics-Ecology Program, Marine Biological Laboratory — exterior view, left valve. X 2 1/3.

Figure 51. *Nucula proxima* variety *truncula* (Dall, 1898), Buzzards Bay, Massachusetts, Sta. "R," coll. H. L. Sanders, Woods Hole Oceanographic Institution — exterior view, left valve. X 4 2/3.

Figure 52. *Periploma leanum* (Conrad, 1831), Martha's Vineyard, Chappaquidick Island, Massachusetts, MCZ No. 192934 — interior view, left valve. X 1/6.

Figure 53. *Petricola pholadiformis* (Lamarck, 1818), Black Beach, West Falmouth, SEP-949, George M. Gray Museum, Systematics-Ecology Program, Marine Biological Laboratory — exterior view, left valve. X 2 1/3.

Figure 54. *Pitar cordata* (Schwengle, 1951), off Port Aransas, Texas, 80 m, MCZ No. 194372 — interior view, right valve. X 2/3.

Figure 55. *Pitar morrhuana* (Linsley, 1845), Hadley Harbor, Elizabeth Islands, Massachusetts, Sta. P-189-64, Systematics-Ecology Program, Marine Biological Laboratory — exterior view, left valve. X 2 1/3.

Figure 56. *Saxidomus nuttalli* (Conrad, 1837), Gulf of Georgia, British Columbia, Canada, MCZ No. 5235 — interior view, right valve. X 1/3.

Figure 57. *Solemya velum* (Say, 1822), Hadley Harbor, Elizabeth Islands, Massachusetts, Sta. P-225-65, Systematics-Ecology Program, Marine Biological Laboratory — exterior view, left valve. X 2 1/3.

Figure 58. *Tagelus divisus* (Spengler, 1794), Hadley Harbor, Elizabeth Islands, Massachusetts, Sta. P-21-63, Systematics-Ecology Program, Marine Biological Laboratory — exterior view, left valve. X 2 1/3.

Figure 59. *Yoldia limatula* (Say, 1831), Hadley Harbor, Elizabeth Islands, Massachusetts, Sta. P-267-65, Systematics-Ecology Program, Marine Biological Laboratory — exterior view, left valve. X 2 1/3.

TABLE 1

DISTANCE BETWEEN GENERA WHEN CONSIDERED AS POINTS IN FACTOR SCORE SPACE

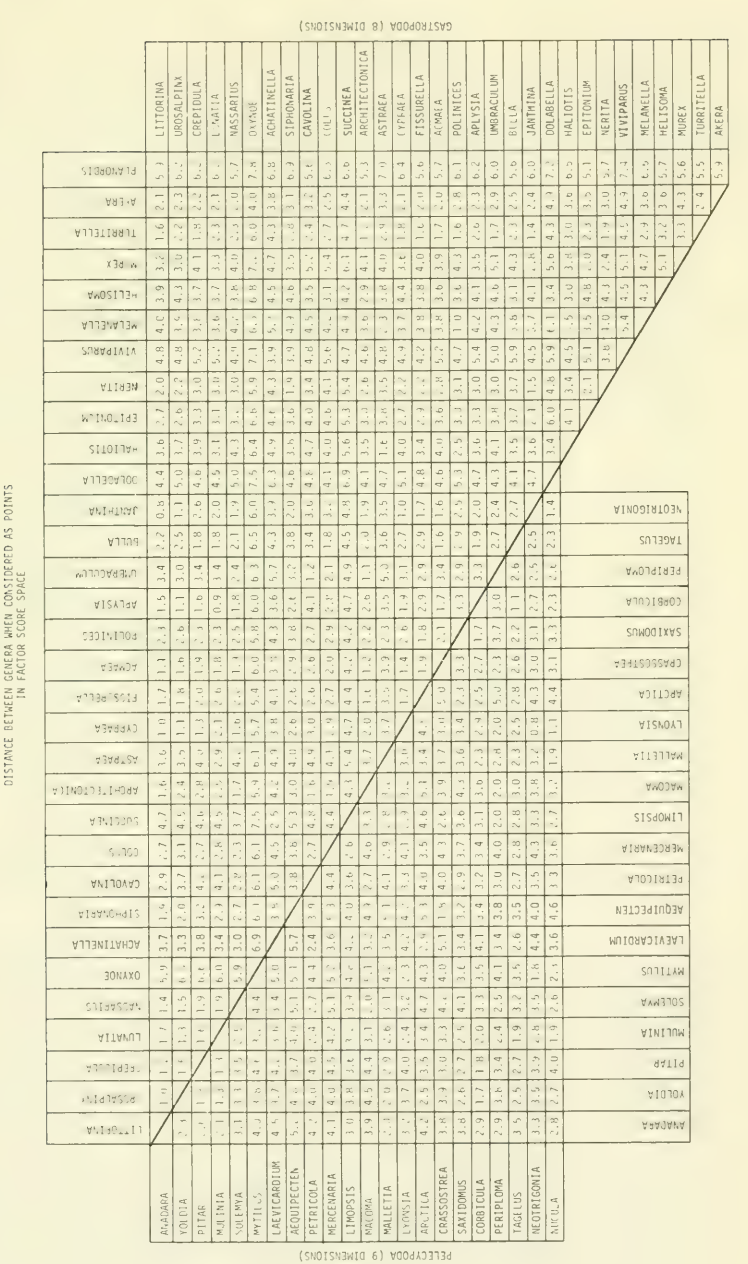

PELECYPODA (9 DIMENSIONS)
GASTROPODA (8 DIMENSIONS)
ANADARA
VOLDIA
PTILA
MULINIA
SOLEMYA
MYTILUS
LAEVICARDIUM
AEQUIPECTEN
PETRICOLA
MERCENARIA
LIMOPSIS
MACOMA
MALLETIA
LYONSIA
ARCTICA
CRASSOSTREA
SAXIDOMUS
CORBICULA
PERIPLOMA
TAGELUS
NEOTRIGONIA
NUCULA
ARCIDAE
NUCULIDAE
NEILONELLIDAE
PHACOIDIDAE
LUCINIDAE
UNGULINIDAE
CARDIIDAE
CRASSATELLIDAE
VENERIDAE
MACTRIDAE
MESODESMATIDAE
CORBULIDAE
PANDORIDAE
GASTROCHAENIDAE
HIATELLIDAE
MYIDAE
PHOLADIDAE
PETRICOLIDAE
ADAPEDONTIDAE
PHOLADIDEA
TRIDACNIDAE
CARDITIDAE
CRYPTODONTIA
PROTOBRANCHIA
FILIBRANCHIA
EULAMELLIBRANCHIA
SEPTIBRANCHIA
ANOMALODESMATA
PALEOTAXODONTA
ARCHEOGASTROPODA
MESOGASTROPODA
NEOGASTROPODA
PULMONATA
OPISTHOBRANCHIA
LITTORINA
UROSALPINX
CREPIDULA
LAMELLARIA
NASSARIUS
OXYNOE
ACHATINELLA
SIPHONARIA
CAVOLINA
CYMBULIA
HELISOMA
MURICANTHUS
TURRITELLA
AKERA
PLANORBIS
AMPHIBOLA
MELAMPUS
MYSTILUS
ACTAEON
ACTEOCINA
HAMINOEA
BULLA
JANTHINA
LIMACINA
CYMBULIA
PTEROTRACHEA
ATLANTA
CARINARIA
PTEROPODA
HETEROPODA
ACTEONIDAE
RINGICULIDAE
ATYIDAE
SCAPHANDRIDAE
BULLIDAE
HAMINOEIDAE
GASTROPTERIDAE
ONCHIDIIDAE
AMPHIBOLIDAE
OTINIDAE
SIPHONARIIDAE
ELLOBIIDAE
PYRAMIDELLIDAE
ACTAEONIDAE
CYLICHNIDAE
DIAPHANIDAE
HAMINOEIDAE
ATYIDAE
RINGICULIDAE
PHILIN

TABLE 2

AMINO ACID RATIOS PER 1000 TOTAL

	Chaetopleura Mantle	Chaetopleura Shell	Spirula Shell	Sepia Shell (cuttle bone)	Loligo Shell (pen)	Nautilus Shell	Haliotis Shell	Nucula Shell	Mytilus Shell	Neopilina Shell with periostracum	Portunid Crabs* Uncalcified Integument	Portunid Crabs* Calcified Integument
OH-Proline	58	--	--	--	--	--	--	--	--	--	--	--
Aspartic Acid	50	128	130	116	74	83	164	69	112	61	102	81
Threonine	21	60	57	43	40	14	22	16	16	23	63	57
Serine	35	68	144	98	52	110	110	73	98	59	69	91
Glutamic Acid	69	98	117	73	44	49	59	35	38	39	113	94
Proline	99	93	71	107	151	8	41	25	14	59	93	103
Glycine	264	131	103	120	131	338	200	453	289	376	133	113
Alanine	136	88	66	106	158	231	144	120	241	50	68	115
Cystine [half]	3	14	31	28	0.2	9	0.4	13	11	2	--	3
Valine	48	45	39	40	65	16	25	20	27	74	44	65
Methionine	7	12	10	10	10	4	5	20	6	15	6	7
Isoleucine	28	30	25	20	24	15	15	12	16	41	37	28
Leucine	65	52	43	51	69	25	26	33	48	98	47	49
Tyrosine	0.6	31	25	60	68	12	33	4	20	1	28	25
Phenylalanine	19	37	27	21	26	54	30	48	17	29	46	30
OH-Lysine	4	--	12	--	16	0.4	0.4	0.7	--	0.3	--	3
Lysine	31	41	31	38	55	2	29	19	18	16	31	52
Histidine	0.4	11	4	49	8	0.4	7	11	5	5	34	26
Arginine	63	61	65	22	8	28	89	27	24	50	80	35
Protein Hexosamines	45.96	0.98	2	2	2	30	13	274	219	160	1.53	.40

* Geometric means - 3 species uncalcified, 6 calcified. Protein/hexosamine arithmetic means.

TABLE 3

FACTOR SCORES. GASTROPODA.

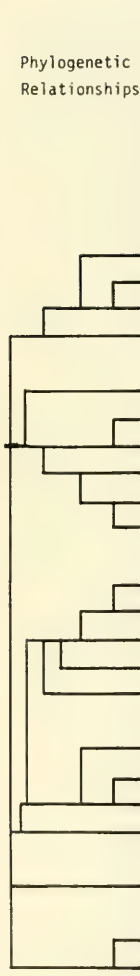
(Shell Tissues)

Phylogenetic Relationships	Varimax Factors		1	2	3	4	5	6	7	8
		Positive Loading	GLY	VAL ISOLEU LEU	OHLYS LYS HIS TYR	PRO		SER ALA	OHPRO	
		Negative Loading	GLU THR MET			ARG	CYS	PHE		ASP
?	SIPHONARIA		-0.8	-0.2	-0.6	-0.5	-0.3	-2.1	0.1	0.1
	HELISOMA		2.2	-0.4	0.3	0.7	0.9	0.2	-0.3	-1.7
?	PLANORBIS		0.6	0.9	5.2	0.9	-0.2	0.8	0.5	-0.3
	ACHATINELLA		1.8	2.0	-0.4	-0.7	0.6	-1.7	-0.3	1.2
	SUCCINEA		3.0	2.0	-0.4	0.8	0.2	-0.1	-0.7	1.4
	CAVOLINA		-0.3	-0.2	0.2	2.5	0.1	-0.1	0.0	-0.3
	UMBRACULUM		-0.6	-0.4	-0.3	1.7	-0.2	0.0	-0.4	-0.5
	ARCHITECTONICA		-0.2	-0.1	0.2	1.0	0.1	0.1	-0.2	-0.5
	AKERA		-0.1	0.6	-0.5	-0.0	0.4	0.2	1.4	-0.2
	OXYNOE		-0.4	0.4	-0.5	0.3	0.4	-0.2	5.6	-0.1
	APLYSIA		-0.6	1.1	-0.4	-1.2	-0.1	-0.2	-0.2	-0.6
	BULLA		-0.0	1.0	0.0	-0.2	-0.1	0.9	-0.6	-1.3
?	DOLABELLA		0.4	-1.3	0.0	-0.1	0.4	-1.1	-0.6	-3.9
	EPITONIUM		-1.0	-0.5	1.5	-0.7	0.5	0.3	-0.3	1.4
	JANTHINA		-1.0	-0.1	0.0	-0.3	0.4	-0.5	-0.3	0.4
	TURRITELLA		-0.4	-0.7	0.2	0.3	0.1	0.3	-0.3	-0.1
	MUREX		-0.8	-0.7	1.8	-2.1	0.9	-0.8	-0.6	0.7
	UROSALPINX		-0.8	0.7	-0.3	-0.9	0.1	-0.5	-0.3	0.3
	NASSARIUS		-0.3	1.4	-0.2	0.3	0.1	-0.3	-0.2	0.1
	COLUS		0.2	0.8	-0.9	1.0	-0.6	0.5	-0.1	-1.4
	MELANELLA		0.9	-1.3	-0.5	-0.6	-0.1	2.2	0.2	1.1
	POLINICES		0.2	-0.7	-0.5	0.7	0.2	1.2	0.1	0.7
	LUNATIA		-0.1	0.8	-0.4	-1.3	0.4	0.2	-0.2	-0.4
	LITTORINA		-1.0	0.4	-0.2	-0.2	0.3	-0.5	-0.3	-0.2
	CYPRAEA		-1.2	0.4	-0.6	-0.1	-0.1	-0.3	-0.1	0.5
	CREPIDULA PLANA		-0.6	0.8	-0.7	0.2	-0.1	0.2	-0.6	-0.3
	CREPIDULA FORNICATA		-0.6	1.6	-0.3	-1.1	-0.8	0.1	-0.6	-0.5
?	FISSURELLA		-0.8	-0.5	0.5	0.2	-0.1	-0.7	-0.1	0.2
?	ACMAEA		-0.7	0.9	-0.2	0.4	0.1	0.2	-0.3	-0.2
	VIVIPARUS		2.3	-1.6	-0.1	0.4	0.5	-2.9	0.1	1.3
	NERITA		-0.8	-1.0	0.6	-0.4	0.3	-1.1	0.2	0.6
	ASTRAEA		1.0	-1.6	-0.7	-1.8	0.0	0.9	0.5	-0.2
	HALIOTIS		1.2	-1.8	0.0	-1.5	0.1	0.0	0.2	-1.3

TABLE 4

FACTOR SCORES. PELECYPODA.

(Shell Tissues)



Phylogenetic Relationships	Varimax Factors		1	2	3	4	5	6	7	8	9
		Positive Loading	THR GLU PRO	VAL	LYS HIS ARG	ALA	ISOLEU LEU VAL HIS	TYR	OHLYS		
		Negative Loading	GLY	SER		MET				ASP	PHE
	PITAR.		0.3	0.3	0.2	-0.5	-0.7	-1.1	-0.4	-1.9	-0.9
	MERCENARIA		2.4	-1.0	1.8	0.2	-1.1	1.8	-1.3	1.4	0.4
	SAXIDOMUS		1.3	-1.1	-0.4	0.5	0.5	0.3	-0.2	-0.9	-1.4
	PETRICOLA		0.5	-0.6	-1.0	-1.1	1.5	1.9	-0.2	1.0	-0.9
	LAEVICARDIUM		2.2	0.5	-1.0	-0.8	0.4	-1.2	-1.5	1.6	2.0
	MACOMA		-0.6	0.1	-0.4	-1.8	-0.4	-0.9	-0.1	1.6	0.7
	MULINIA		0.1	0.7	-0.5	-0.2	-0.5	0.1	-0.1	-1.0	0.3
	TAGELUS		0.8	-0.6	-0.5	0.1	-1.0	0.0	0.0	0.3	-0.4
	CORBICULA		0.7	-0.3	-0.3	0.4	-0.8	1.6	-0.3	-0.7	0.9
	ARCTICA		2.9	0.3	-0.5	1.1	-0.1	1.1	4.8	-0.4	0.0
	AEQUIPECTEN		-0.6	-3.1	-0.5	-0.6	-0.6	-0.7	0.1	-1.5	1.9
	CRASSOSTREA		-0.9	-2.1	0.3	-0.5	-1.2	1.2	-0.2	-0.6	1.2
	MYTILUS		-0.8	-0.3	-0.6	3.0	0.5	0.0	-0.4	0.4	1.0
	ANADARA		-0.5	1.3	1.7	0.1	-0.2	1.4	0.1	-0.4	-0.1
	LIMOPSIS		0.1	-1.2	2.0	-0.8	-0.5	-1.8	-0.3	0.8	-2.3
	NEOTRIGONIA		-1.1	-0.8	0.1	1.5	0.0	-1.0	1.2	0.7	0.2
	PERIPLOMA		-1.2	-0.6	0.6	-0.8	-0.4	2.6	-0.4	0.9	-1.8
	LYONSIA		-1.1	-0.6	0.2	1.1	0.0	0.3	0.3	1.2	-1.4
	NUCULA		-0.6	0.1	0.2	0.7	-0.7	-0.7	0.0	1.0	-0.9
	SOLEMYA		-0.9	1.3	-0.8	-1.1	0.2	-0.7	0.2	0.8	-0.6
	MALLETIA		0.5	1.0	0.9	0.2	-1.5	-0.3	-0.5	0.6	0.4
	YOLDIA		0.9	1.2	0.2	0.6	-0.6	-0.1	0.2	-1.2	-0.2

TABLE 5

AMINO ACID RATIOS PER 1000 TOTAL

	Nerita	Viviparus	Archi-tectonica	Siphonaria	Helisoma	Planorbis	Succinea	Achatinella
	Marine	Fresh Water	Marine	Marine	Fresh Water	Fresh Water	Land	Land
OH-Proline	--	--	--	--	--			--
Aspartic Acid	103	48	132	133	143	98	11	47
Threonine	50	11	57	46	23	56	11	16
Serine	70	34	88	58	74	61	37	25
Glutamic Acid	114	26	114	103	69	91	9	29
Proline	85	54	90	82	39	59	57	50
Glycine	116	519	159	116	380	114	526	411
Alanine	108	16	81	74	62	88	19	30
Cystine [half]	2	8	15	16	3	21	4	4
Valine	48	17	40	63	38	61	83	78
Methionine	26	11	19	30	3	10	1	2
Isoleucine	23	26	36	35	15	37	50	64
Leucine	68	59	76	76	50	56	121	110
Tyrosine	23	46	14	15	42	67	28	11
Phenylalanine	44	95	19	74	17	--	16	74
OH-Lysine	1	--	3	--	1	16	--	0.3
Lysine	36	15	26	34	25	82	12	39
Histidine	16	9	6	1	1	34	0.2	0.2
Arginine	67	6	25	45	15	48	6	9
Protein								
Hexosamine	66	1060	22	23	11	n.d.	77	82

BREVIORA

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THE HYDROID OF *VANNUCCIA FORBESII* (ANTHOMEDUSAE, TUBULARIIDAE)

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ABSTRACT: This paper deals with a hydroid of the order Anthomedusae (Athecatae), family Tubulariidae, formerly described as *Hybocodon forbesii* Mayer 1894. The structure of the hydroid proves that the species does not belong to the genus *Hybocodon;* a new genus, *Vannuccia,* is therefore introduced. The hydroid, the budding medusae, the asexual reproduction and the young medusae are described in this paper.

INTRODUCTION

During the preparation of a monograph of the Anthomedusae and athecate hydroids from the Gulf of Naples a tubularian hydroid was found on mud in the Bay of Naples. This hydroid liberated medusae, in the laboratory, which appeared to belong to the species *Hybocodon forbesii* Mayer 1894.

But since the hydroid does not have the structure of other *Hybocodon* hydroids and does not resemble any other hydroid of the Tubulariidae, a new genus had to be established for the former *Hybocodon forbesii.* The new genus is named *Vannuccia,* in recognition of Dr. Martha Vannucci, the head of the plankton section of the Oceanographic Institute of Sao Paulo, who has done extensive research on the plankton around the Brazilian coast.

The find reported here is the first and only case in which *Vannuccia forbesii* (Mayer) has been recorded from the Mediterranean. Only one specimen of the hydroid stage could be found and no free medusae were collected from the sea. However, the species proved easy to keep in the laboratory, and numerous medusae as well as hydroids were liberated from the one specimen.

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Vannuccia n. gen.

Type species. Vannuccia forbesii (Mayer) 1894: 236, pl. I, fig. 1; the gender of the new generic name is feminine.

Generic characters. Tubulariidae with solitary hydroids with one whorl of moniliform oral tentacles and an aboral whorl of filiform tentacles. With endodermal stem canals and basal tuft of rooting filaments. Medusa buds borne on blastostyles just above the aboral tentacle whorl. Free medusae with one tentacle and no exumbrellar cnidocyst rows.

Vannuccia forbesii (Mayer)

Hybocodon forbesii Mayer, 1894: 236, pl. I, fig. 1.

Specific characters. Hydroid with 12 to 14 oral tentacles and 16 to 20 aboral tentacles. Asexual reproduction by transverse fission of the stem. Free medusae with slight asymmetrical bell, one fully developed tentacle with a large terminal cnidocyst swelling.

Distribution. Tortugas, Bahama Islands, and Florida (Mayer, 1894; 1910); Trivandrum and Madras, India (Nair, 1951); southern Japan (Uchida, 1927); Bay of Naples, Mediterranean.

Description of the species. The hydroids of *V. forbesii* are very similar to those of *Corymorpha nutans.* The hydranth of *V. forbesi* consists of a stem or hydrocaulus and the hydranth body itself. The base of the stem or the "foot" (Fig. 6) shows a similar arrangement of rooting filaments and endodermal canals to that seen in *Corymorpha nutans.* The whole stem is surrounded by a flexible perisarc which extends slightly below the hydranth body. There the perisarc is usually marked by a slight constriction of the stem (Fig. 1).

The length of hydranth and stem measures 2-3 cm for specimens with medusae buds, but there is great variability in the length of the stem.

The oral tentacle whorl consists of 12 to 14 tentacles each of them carrying 4 to 6 cnidocyst swellings. The aboral tentacle whorl consists of 16 to 20 tentacles. Each aboral tentacle is very long and has a small swelling at its tip which is more or less pronounced depending on whether the tentacles are contracted or expanded.

Figure 1. *Vannuccia forbesii,* adult hydroid with medusae buds. Drawn by Ilona Richter.

The medusa buds develop in clusters on short blastostyles. As the buds are naked, the one tentacle of each bud can be seen in the more advanced stages of the medusa formation. The liberated medusae are 1.8-2.0 mm high. The exumbrella is apple shaped and somewhat asymmetrical. Young medusae show all the features of the specific characters of the adult medusae with the exception of the gonads, which develop later. This is typical of the *Corymorpha-Tubularia* group.

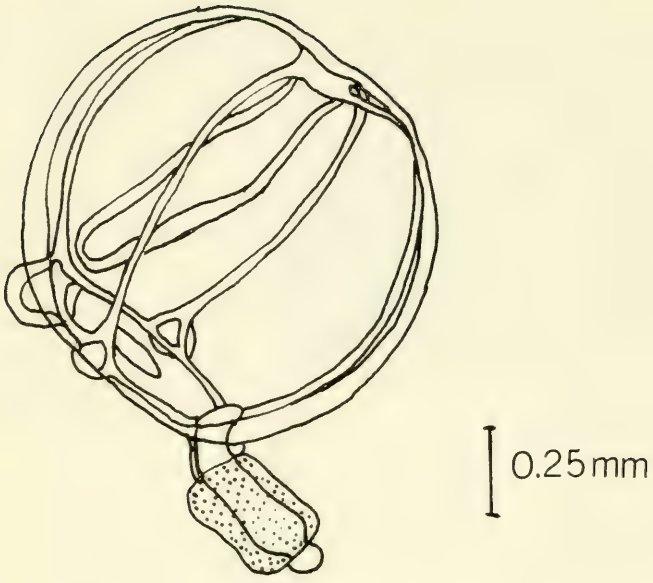

Fig. 2. *Vannuccia forbesii,* male medusa two days old. Drawn by Ilona Richter.

Medusae of *V. forbesii* carry one fully developed tentacle and three tentacle bulbs. The tentacle bulb which is opposite the fully developed tentacle is larger than the other two (Fig. 2). This bulb starts to grow out on the second day after liberation to form a small rudimentary tentacle. Mayer, who gives a description of a fairly young and an adult medusa of *V. forbesii* (Mayer, 1894; 1910), shows that this tentacle may grow longer in fully mature specimens (Mayer, 1910, pl. III). The one fully developed tentacle has a large swelling at its tip, which is provided with numerous cnidocysts. The manubrium is club shaped without a peduncle and extends to the velum. Usually the manubrium does not stay in the center of the subumbrellar cavity, as is generally expected of anthomedusan species, but is located slightly nearer the tentacle bulb opposite the fully developed tentacle. The gonads start to develop soon after the liberation of the medusa. The stomach is completely encircled by the gonads. As the medusae are difficult to feed, I did not manage to get specimens with fully mature gonads. The velum is thin and narrow.

Figure 3. *Vannuccia forbesii*, three developmental stages of young hy-

Reproduction and development. All of my medusae of *V. forbesii* were males. Therefore, the sexual reproduction could not be observed. However, there is a very interesting type of asexual reproduction of the hydroid: the base of the foot of the hydroid thickens slightly and is then constricted off from the remainder of the stem (Fig. 3), and is freed from the perisarcal sheath. It develops four oral and six aboral tentacle buds after it is freed (Fig. 4). Sometimes, however, the tentacle buds are already developed inside the perisarc of the old hydranth. A similar type of

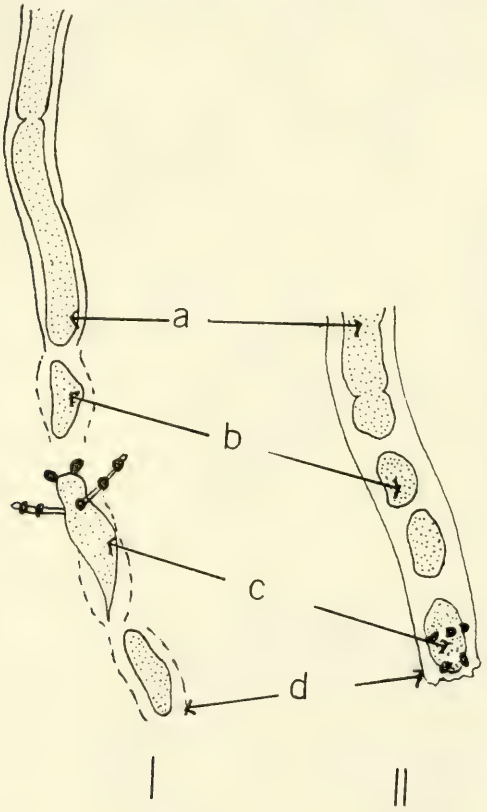

Figure 4. Comparison between the asexual budding of *Euphysa aurata* and *Vannuccia forbesii.* I, *Euphysa aurata;* II, *Vannuccia forbesii.* a, Hydranth stem; b, young buds which are constricted off from the foot of the hydranth; c, developing young hydranths; d, perisarc. For the clarity of the figure the rooting filaments are omitted in II.

budding is known from *Euphysa aurata* (Forbes) and *Hypolytus peregrinus* Murbach. But in *Euphysa aurata* the oral tentacles of the bud always develop distal to the aboral ones, in relation to the "mother" stem (Fig. 3).

The liberated hydranths do not settle immediately but move around slowly until they affix themselves after some hours or even one or two days. This asexual reproduction may become so prolific that a whole tuft of hydroids is formed out of one specimen in about a week.

Ecological observations. When found in May 1962, the young hydroid of *V. forbesii* had only six oral and ten aboral tentacles. During its development the number of tentacles increased. The young one was found in mud at 30 m depth. In the same region I found *Euphysa aurata,* but no other hydroids or medusae of *V. forbesii.* The hydroid was kept at 18°C. The asexual reproduction started at once, after the hydroid had been brought to the laboratory. Medusae production took place in autumn and winter. The asexual reproduction did not cease while the development of medusa buds was taking place.

SYSTEMATIC DISCUSSION

The medusae which were liberated from the above described hydroid match Mayer's description of *Hybocodon forbesii* (Mayer, 1894), with one exception: There is a velum in our specimens. But then, while Mayer says in his original description "without velum" in 1894, his redescription, based on more abundant material, in his "Medusae of the World" (Mayer, 1910:42) mentions: "The velum is narrow."

Mayer placed his medusa species in the genus *Hybocodon* on account of the slightly asymmetrical bell and the one tentacle. Kramp is the first one to question the placement of *Hybocodon forbesii* in the genus *Hybocodon,* suggesting however that it should provisionally remain in that genus (Kramp, 1959, 1961). The medusa stage is somewhat reminiscent of *Euphysa* and *Corymorpha* as well.

Regarding the hydroid stage, difficulties arise about placing the species in the proper systematic position. The morphology of the hydroid demands that the species (up to now known from its medusa stage only) not remain in the genus *Hybocodon* any more, because it is certainly not a *Hybocodon* hydroid. The establishment of the new genus *Vannuccia* for the former *Hybocodon forbesii* is suggested therefore.

The combination of moniliform oral and filiform aboral tentacles in *V. forbesii* hydroids is unique among the Tubulariidae. Yet, upon checking the different solitary tubulariid hydroids, either from literature or preserved material, I find that the hydroid of *V. forbesii* bears some relationship to *Hypolytus obvoluta* (Kramp) 1933; this was first described as *Corymorpha obvoluta,* and later placed in the genus *Hypolytus* by Rees, being cogeneric with *H. peregrinus* Murbach 1899, on account of the moniliform tentacles in both sets (Rees, 1957). However, if one compares the figures of *H. peregrinus* Murbach and *H. obvoluta* (Kramp), it seems that the aboral tentacles of *H. obvoluta* are much less moniliform than the aboral tentacles of *H. peregrinus.* This points to a certain

Figure 5. Oral tentacles of young *Vannuccia forbesii* (I), and young *Corymorpha nutans* (II).

order insofar as there are: (1) moniliform tentacle whorls in both sets in *H. peregrinus* Murbach, (2) "reduced" aboral moniliform tentacles in *H. obvoluta* (Kramp), (3) filiform aboral and moniliform oral tentacles in *Vannuccia forbesii,* and (4) filiform tentacles in both whorls, slightly moniliform in the oral set when young, in *Corymorpha nutans.* In this comparison, *Vannuccia* is placed between *Hypolytus* and *Corymorpha.* There are also other characters indicating the relationship of *Vannuccia forbesii* with *H. obvoluta,* on the one hand, and with *Corymorpha nutans,* on the other: *Hypolytus obvoluta* shows faint endodermal channels; they are more apparent in *V. forbesii* and strongly developed in *C. nutans.* Similarly, the anchoring filaments are feebly developed

in *Hypolytus obvoluta,* become more apparent in *Vannuccia forbesii,* and are strongly developed in *Corymorpha nutans.*

In summary, the genus *Vannuccia* is related to the genera *Hypolytus* and *Corymorpha,* representing an intermediate stage between them. Medusa and hydroid of *Vannuccia forbesii* are decidedly different from those of either genus, so that the new genus, *Vannuccia* may be justified.

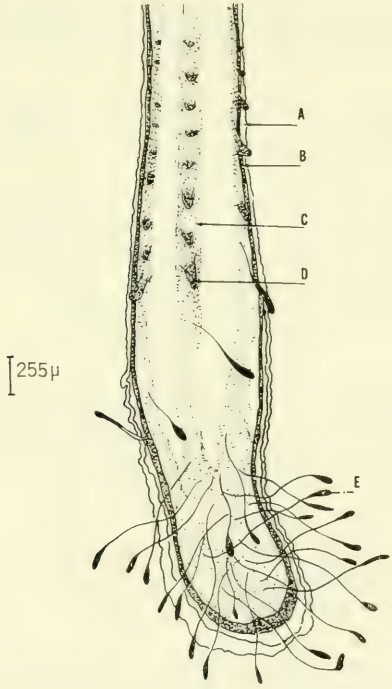

Figure 6. *Vannuccia forbesii,* base of hydranth stem. The rooting filaments form a dense tuft, but in order to make the figure clearer only a few of them are drawn in this figure. A, Gelatinous perisarc; B, ectoderm; C, endodermal ridge; D, developing rooting filament; E, rooting filament.

The genus *Vannuccia* is closer to *Corymorpha* than to *Tubularia.* If the family Tubulariidae is divided into two families, the Corymorphidae and Tubulariidae (Rees, 1957; Brinckmann-Voss, MS in preparation), the genus *Vannuccia* would have to be placed in the Corymorphidae.

ACKNOWLEDGMENTS

I wish to thank Mrs. Sofia Giaquinto-Boag for her most efficient help in maintaining the polyps, and the director of the Naples Zoological Station, Dr. P. Dohrn, for his generous support.

REFERENCES CITED

Allman, G. J.

1872. A monograph of the gymnoblastic or tubularian hydroids. Ray Society, London: 1-450, 84 figs., 32 pls.

Kramp, P. L.

1933. Coelenterata, Ctenophora and Chaetognatha. The Scoresby Sound Comm. 2nd East Greenland Exped. in 1932. Meddel. om Grønland., **104**(11): 1-20.

1949. Origin of the hydroid family Corymorphidae. Vidensk. Medd. fra Dansk Natur. Foren., **111**: 183-215.

1959. The Hydromedusae of the Atlantic Ocean and adjacent waters. Copenhagen. Dana Report No. **46**: 1-283.

1961. Synopsis of the medusae of the world. J. Mar. Biol. Assoc. United Kingdom, **40**: 1-469.

Mayer, A. G.

1894. An account of some medusae obtained in the Bahamas. Bull. Mus. Comp. Zool., Harvard College, **25**(11): 235-242, 3 pls.

1910. Medusae of the world. Part I, Hydromedusae. Carnegie Inst. Washington, Publ. **109**(1): 1-230, 29 pls.

Murbach, L.

1899. Hydroids from Wood's Holl, Mass. *Hypolytus peregrinus*, a new unattached marine hydroid. Quart. J. Microscop. Sci., (N.S.) **42**: 341-360.

Nair, K. K.

1951. Medusae of the Trivandrum Coast, Part I, Systematics. Bull. Centr. Res. Inst. Univ. Travancore (Trivandrum), 2 C (Nat. Sci.) No. **1**: 47-75.

Rees, W. J.

1957. Evolutionary trends in the classification of capitate hydroids and medusae. Bull. Brit. Mus. (Nat. Hist.), Zool., **4**(9): 453-534.

Uchida, Th.

1927. Studies on Japanese Hydromedusae. I, Anthomedusae. J. Imp. Univ. Tokyo, Sect. 4, Zool., **1**: 145-241, 47 figs., 2 pls.

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BREVIORA

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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA

III. TWO NEW GOMPHODONTS, *MASSETOGNATHUS PASCUALI* AND *M. TERUGGII*

By Alfred Sherwood Romer

In previous numbers of this series an account was given of the 1964-1965 expedition of the Museo de la Plata and the Museum of Comparative Zoology to the Permo-Triassic of western Argentina, and the Permo-Triassic geology of the Chañares-Gualo region was briefly described (Romer, 1966; Romer and Jensen, 1966). This and succeeding papers will be devoted to descriptions of the new genera and species contained in the Chañares fauna.

Owing to a sequence of political incidents which need not be detailed here, the greater part of the collection has only recently (December 1966) reached the Museum of Comparative Zoology after the lapse of nearly two years. The one box of specimens which reached Cambridge earlier and is now partially prepared, contains, however, a considerable variety of reptilian remains, particularly skulls and jaws. Represented, in addition to indeterminate fragmentary materials, are a small pseudosuchian, a moderately large dicynodont with powerful tusks, two carnivorous cynodonts, and at least four (possibly more) gomphodont cynodonts. For most of these forms, the materials at hand are none too complete, even as regards crania and dentitions, and it hence seems wise to defer description until the arrival of the main body of the collection, in which further specimens are almost surely present. Two of the gomphodonts, however, are represented by a number of well-preserved skulls and jaws, and will be described here as *Massetognathus pascuali* and *M. teruggii*. As will be seen from the descriptions and illustrations, the two are comparable in many ways, and are obviously closely allied. The skulls assigned to *M. teruggii* are on the average about 43 per cent larger than

those of *M. pascuali,* and the differences between the two are in great measure differences which might reasonably be associated with the contrast in size. I was at first inclined to believe that we were possibly dealing with growth stages of a single form. However, the skulls sort clearly into two size groups, rather than forming the graded series expected had they represented growth stages of a single species. The difference in size between the two is considerably greater than that expected in sex differences, and it is hence reasonable to believe that we are dealing with two species of a single genus.

MASSETOGNATHUS gen. nov.

Type species: *M. pascuali* sp. nov.

Diagnosis. Traversodontid gomphodonts of modest size, known skull lengths (snout to condyles) ranging from 82 to 138 mm. The skull is short and broad, the width about seven-tenths the length to condyles. Muzzle expanded laterally so that the maxilla is broadly exposed ventrally lateral to the cheek tooth row. As in gomphodonts generally, the zygomatic arch is broad but with a constricted posterior base; the arches widely expanded for their full length in a line parallel to the long axis of the skull; the epipterygoid-pterygoid bar extending broadly back to the quadrate region; the angular process of the dentary well developed and thickened at its ventral border; posterior to this, the angular-surangular well exposed laterally. No suborbital process of the jugal; external exposure of the squamosal on the zygomatic arch restricted to upper and posterior borders; no posterior projection of the angular process of the dentary. Four upper, three lower incisors; canines modestly developed; 12-15 upper, 11-13 lower cheek teeth; anterior teeth smaller and simpler in structure than main series, but no distinct "premolar" series. Teeth of typical traversodont pattern; upper "molars" with two lateral cusps, the more posterior one the more prominent; a high posterior transverse ridge with cusps close to and at the posteromedial corner. Teeth subquadrate, but extending farther laterally toward the posterior corner; anterior and posterior margins essentially transverse and parallel, but slightly convex in outline anteriorly toward the external margin and similarly concave posteriorly, so that each tooth "shoulders" to a slight degree into the area of its next anterior neighbor. The generic name (masculine) refers to the obviously excellent chewing powers of the jaws.

MASSETOGNATHUS PASCUALI sp. nov.

Holotype. No. 65-XI-14-1, Museo de la Plata, skull and jaws, collected by the 1964-1965 expedition of the Museo de la Plata and the Museum of Comparative Zoology.

The specific name is in honor of Dr. Rosendo Pascual, Professor of Paleontology in the Universidad de la Plata, who accompanied the expedition during much of its stay in western Argentina, and was exceedingly helpful to us before, during, and after our field work.

Horizon and locality. From an exposure in the Triassic Chañares Formation about two miles north of the point where the Chañares River debouches into the Campo de Talampaya, in western La Rioja Province, Argentina.

Diagnosis. A small form, with a mean length, snout to condyles, of about 87 mm in available specimens. Posterior portion of frontals and anterior portion of parietals form a flat triangular dorsal area, the posterior end of the triangle extending back to a parietal foramen of modest size; the postorbitals extend back on either side to a point about opposite the parietal foramen. The angular process of the dentary descends to form approximately a right angle with the ventral margin of the bone. Twelve upper and 11 lower cheek teeth in available specimens.

Description. Massetognathus pascuali appears to be an exceedingly common member of the Chañares fauna; even in the restricted material currently available from our collection there are some seven fairly good skulls, as well as less complete skull and jaw specimens and considerable postcranial material. This is a relatively small animal, the mean length of available specimens, from premaxilla to occipital condyle (allowing for minor anterior or posterior deficiencies), being 87.3 mm, with a range from 82 to 95 mm. As noted above, the first thought that these specimens might be growth stages leading to *M. teruggii* appears to be negated by the fact that the series here assigned to *M. pasuali* seems to cluster closely about the size mean, with an average deviation of but 3.6 mm, or about 4 per cent.

The general nature of the skull is obvious from Figures 1-3. Its structure is for the most part that familiar in advanced cynodonts generally and gomphodonts in particular, and in many regards does not call for detailed description. In its general proportions it is relatively broad and short. The seeming shortness is exaggerated by the most distinctive feature of the genus – the "swollen" muzzle. As in all typical gomphodonts, the two tooth rows of the cheek

battery are close together on the ventral surface of the skull. In most gomphodonts there is little lateral extension of the muzzle beyond the line of the tooth row, and (as may be seen, for example, in *Diademodon* or *Exaeretodon*) the snout region is slender. Here, however, the maxillae extend far out dorsally (with a downward slope) to a point about opposite the lower margin of the orbits, then, curving downward and inward, present a broad ventral surface lateral to the tooth rows.

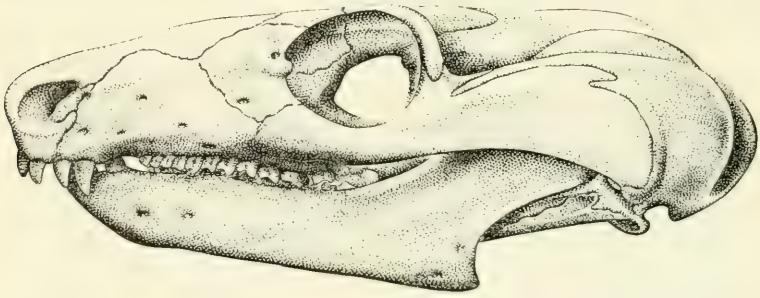

Figure 1. Lateral view of the skull of *Massetognathus pascuali*. Natural size.

The skull is low, and the orbits face somewhat more dorsally than laterally and slightly anteriorly. The prefrontal and postorbital meet broadly above the orbits. The nasals and frontals form an essentially flat dorsal platform atop the skull. On either side, the prefrontals and postorbitals are somewhat raised above the flat surface of the frontals and anterior part of the parietals. Posterior to the orbits, the ridges formed by the postorbitals converge to leave a triangular wedge of flat dorsal surface formed by the back portion of the frontals and the anterior portion of the parietals. This narrows posteriorly, with the rather small parietal foramen at the apex of the triangle. Posterior to this, the conjoined parietals form a sharply developed parietal crest. The postorbitals on either side extend backward, sheathing the parietals laterally, to about the level of the parietal foramen.

The lateral surfaces of the braincase appear to be constricted in typical cynodont fashion; I shall postpone description of this region and the interior of the orbit until further material is available for "dissection" and sectioning. The occipital surface of the skull is of normal cynodont construction. Laterally, as in gomphodonts generally, but in contrast to other cynodonts, the squamosal descends

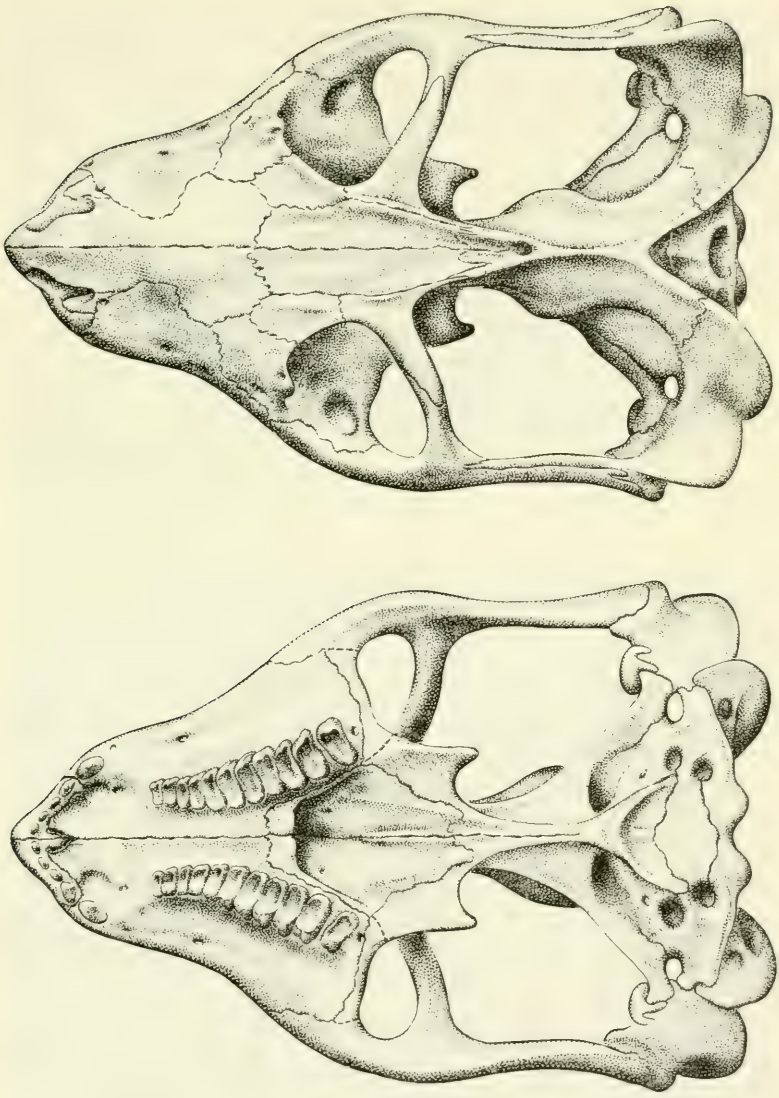

Figure 2. Dorsal and ventral views of the skulls of *Massetognathus pascuali*. Natural size.

ventrally so that the connection between the portion of the bone forming the lateral wing of the occipital region and that associated with the zygoma is only by a narrow neck ventrally; in posterior view, the dorsal margins of the two portions form a V, widely open above. The pterygoid-epipterygoid bar reaches broadly back to the quadrate region above a pterygo-paroccipital fenestra. The squamosal forms the boundaries, medial and lateral, of a distinct

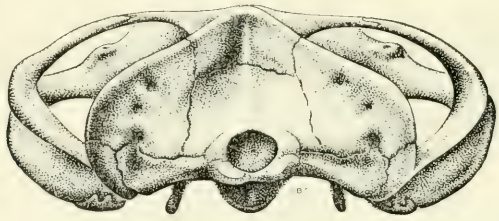

Figure 3. Posterior view of the skull of *Massetognathus pascuali*. Natural size.

external auditory meatus. The postorbital bar is slender; the zygomatic arch, however, is deep dorsoventrally. In contrast to cynognathids, in which the arch slants diagonally outward and backward from the orbital region to attain its greatest length posteriorly, the arch, as in gomphodonts generally, attains its full breadth at the posterior margin of the orbit, and runs back from this point parallel to the main axis of the skull, allowing a high development of the temporal musculature. The external exposure of the squamosal on the arch is restricted to a narrow area at the top of the arch, and, curving downward posteriorly, along the anterior margin of the external meatus.

Ventrally, the two rows of cheek teeth are close together anteriorly, and diverge gently posteriorly. The secondary palate extends back most of the length of the tooth row and (although the sutures are none too certain) the palatines appear to form the most posterior portion of the secondary palate. Back of the secondary palate, little of sutures can be made out in the material available. On either side, the lateral margins of the pterygoids extend backward as raised ridges which terminate in sharply-pointed flanges directed downward and backward. From the median bar formed posteriorly by the conjoined pterygoids and basicranial axis, a pair of ridges run diagonally forward and laterally toward the posterior ends of the tooth rows, and a median ridge runs directly forward.

The posterior ventral structures are of the type commonly seen in cynodonts, with an excavated basioccipital-sphenoid area bounded by a pair of ridges; on either side, there is a well-developed vagal foramen, and farther forward, the fenestra ovalis. A V-shaped channel, bounded medially by the braincase wall and laterally by the pterygoid-epipterygoid bar, represents the primitive cranio-quadrate passage; anteriorly it is roofed below by a median extension of the pterygoid. In most specimens the quadrate (plus quadratojugal, loosely attached to the skull) has dropped out, leaving a pair of notches to represent its area of articulation. In the jaw the dentary is highly developed, with a high and broad coronoid process, a posterior process which reaches back nearly to the articular area, and a pronounced angular process of the dentary which is thickened and rounded ventrally. Posteriorly, in contrast to non-gomphodonts, the angular and surangular are well exposed on the outer surface. The elements of the jaw apart from the dentary are incompletely preserved in the available material, and I shall reserve description of the inner surface of the mandible for a future occasion.

There are four upper and three lower incisors of modest size, somewhat chisel-shaped and with longitudinal striations. The canines are relatively little developed. The cheek teeth are separated from the canines by a short diastema; both above and below, the members of each cheek series (Figs. 4, 6) are crowded close to one another, and the two rows, rather close together in front, curve gently outward posteriorly. As is now well known in other gomphodonts (Crompton, 1955, etc.), the composition of a gomphodont cheek battery may change during "adult" life by the eruption of additional teeth posteriorly and resorption of anterior ones, so that no precise tooth count is possible. In our material there is no positive evidence of anterior resorption, but in most specimens there is evidence of posterior addition in the presence, at the back end of the battery, of either a newly erupted but unworn tooth, one well formed by not yet erupted, or a partially developed tooth still in its alveolus. In the specimens currently available to us there are generally 12 maxillary teeth, and 11 in the only two mandibles now in our possession. Although, in contrast to diademodonts, there is no sharp contrast between small "premolars" and a "molar" series, the more anterior cheek teeth are smaller and with a simpler pattern. The wear on the teeth is obviously great, so that little detail of the crown pattern can be seen except in teeth at the back end of the series which are as yet unerupted or very freshly erupted.

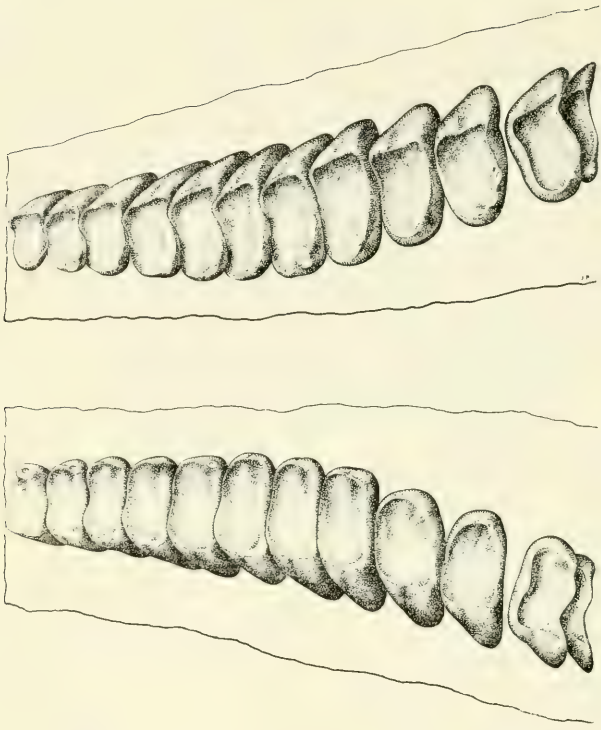

Figure 4. Left (above) and right (below) upper cheek tooth series of a specimen of *Massetognathus pascuali*. X 3.

Such a tooth from the maxillary series is shown in Figure 5. In surface view the crown is subquadrate, nearly twice as broad as long anteroposteriorly. The inner margin is curved; anterior and posterior margins are nearly straight and parallel to one another, except that towards the outer border the anterior margin is somewhat convex, the posterior border opposite somewhat concave. Each tooth thus "shoulders" somewhat into the proper area of its next anterior neighbor – a feature which is much more pronounced in the more advanced traversodonts of the later Ischigualasto horizon. On the outer border, the base of the cone forming the posteroexternal cusp extends considerably outward and backward, so that the external boundary is a diagonal line. The outer portion of the tooth is a high anteroposterior ridge, on which a major cusp develops posteriorly; a minor cusp, only slightly separated from it,

is developed along the downward anterior slope of the ridge. Medial to the two cusps, the external ridge descends abruptly into a basin which occupies most of the crown area. This basin, apart from its straight lateral border, is an essentially oval concave area, without internal markings. It is surrounded on posterior, medial, and anterior borders by a curved ridge, considerably higher along the posterior margin than medially and anteriorly. An elongate cusp is present about two-thirds the way in along the posterior ridge, a second cusp near the posteromedial corner, and a lower cusp part way along the anterior ridge. In a freshly erupted tooth a series of tiny bead-like denticulations may be seen along

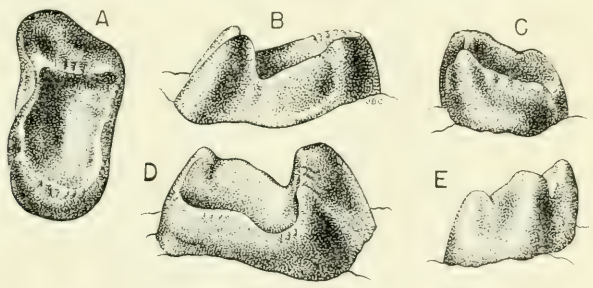

Figure 5. A right upper "molar" of *Massetognathus pascuali*. *A*, Crown view. *B*, Posterior and somewhat ventral. *C*, Medial. *D*, Anterior and somewhat dorsal. *E*, Lateral. X 4.

most of the extent of the ridges surrounding the basin posteriorly, medially, and anteriorly, and a few may even be present along the external ridge. With wear, the denticulations rapidly disappear; with somewhat further wear, the anterior ridge is ground down, leaving the posterior ridge projecting, but with distinction between its two cusps lost, and the internal ridge still prominent. With still further wear, the posterior ridge, too, becomes worn away, and the basins of successive teeth become a continuous surface, flat anteroposteriorly but concave as seen in end view, rising medially to a persistent medial ridge, and rising still higher laterally to the outer longitudinal ridge.

The general position of the lower cheek series corresponds to that above. (Because of imperfections in available specimens of *M. pascuali,* I have shown instead, in Figure 6, that of *M. teruggii.*) As in the upper jaw, the most anterior cheek teeth are smaller and simpler in pattern than the main series, although there is no sharp division into "premolars" and "molars." Just as in the case of

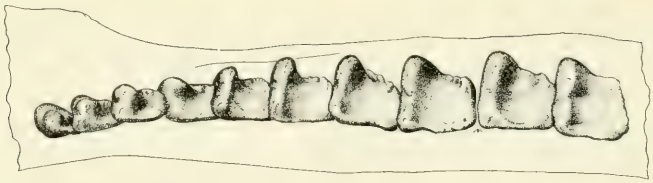

Figure 6. Right cheek tooth series of a specimen of *Massetognathus teruggii*. X 2.

the upper "molars," wear tends to obliterate rapidly most of the details of the crown pattern. A freshly erupted tooth is shown in Figure 7. The lower "molars" are of the diagnostic traversodont pattern. This pattern, as regards position in the jaw, gives them a build contrasting sharply with those of the upper jaw. Curiously, however, if one imagines a lower tooth rotated 90°, so that the anterior border faces, instead, to the outside, the pattern becomes highly comparable to that of the upper tooth. The lower cheek teeth are subquadrate in shape. The anterior portion forms a high transverse ridge, partially subdivided into two cusps, of which the more external is the larger and higher. Just as the external ridge of the upper tooth descends steeply on its inner surface to the basin of the tooth, so here the posterior face of the anterior transverse ridge descends abruptly into the subquadrate, smoothly concave tooth basin. As in the case of the upper tooth, the basin is surrounded by a continuous ridge on the other three

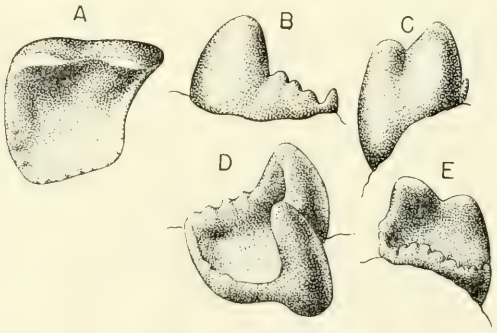

Figure 7. A right lower "molar" of *Massetognathus teruggii*. *A*, Crown view. *B*, Lateral. *C*, Anterior. *D*, Medial. *E*, Posterior. X 4.

sides; the external ridge is much the highest, the internal the lowest. As in the margins of the upper basin, so here a nearly continuous series of bead-like cuspules is present in the unworn tooth, but in contrast to the upper teeth, no conspicuous cusps are present, even in the unworn tooth. With wear, the denticulations soon disappear, and except for the strong anterior cross-ridge, the tooth is reduced to a somewhat concave basin with a somewhat raised rim externally.

MASSETOGNATHUS TERUGGII sp. nov.

Holotype. No. 65-XI-14-2, Museo de la Plata, skull and jaws, collected by the 1964-1965 expedition of the Museo de la Plata and the Museum of Comparative Zoology.

The species is named for Professor Mario Teruggi, who was most helpful in the carrying out of our field work and in our post-expeditionary difficulties.

Horizon and locality. From the same horizon and locality as the type of *M. pascuali.*

Diagnosis. A larger species than *M. pascuali,* with a mean skull length of about 125 mm in available specimens. The flattened dorsal area formed by the frontals and anterior portions of the parietals is more restricted than in *M. pascuali,* the roof constricting to a sagittal crest in front of the parietal foramen, which is reduced to a tiny slit. The postorbitals extend backward on either side of the crest to a point well back of the foramen. The angular process is not as sharply developed as in *M. pascuali,* the posterior and ventral borders of the process meeting at an obtuse angle. Thirteen to 15 maxillary, and 11 to 13 mandibular cheek teeth in available specimens.

Description. M. teruggii seems, next to *M. pascuali,* to be the most common of Chañares reptiles; our present restricted materials contain some five skulls of this form. As noted above, this species is considerably larger (more than 40 per cent) than *M. pascuali.* This is, of course, a considerably greater difference than would be expected if we were dealing with sex differences. The skulls attributed to *M. teruggii,* like those of *M. pascuali,* seem to form a compact series, ranging from 115 to 138 mm in length, with an average deviation from the mean of about 9 mm, or about 7 per cent only.

The skull of this species (Figs. 8-10) is very similar in most regards to that of its associate, *M. pascuali.* Since we have described, above, the skull of this smaller form in some detail, we

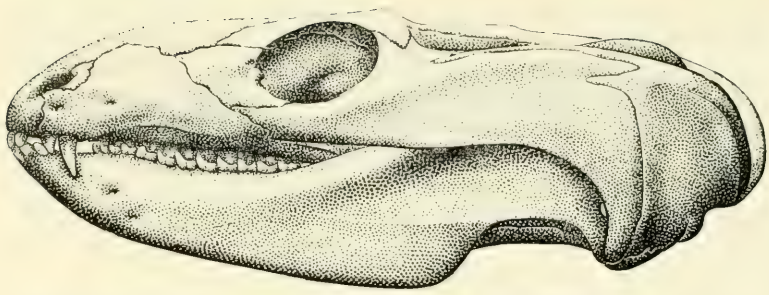

Figure 8. Laterial view of the skull of *Massetognathus teruggii*. X ¾.

can here avoid unnecessary and monotonous repetition of description of their numerous similar features, and call attention only to the few points of difference. These are in part associated with size. As is, I think, well known (and should be obvious), the chewing apparatus of a large form must be disproportionately large as compared with that of a relative of smaller size. Here the differences in this feature have to do with a somewhat greater development of a sagittal crest. This is accomplished by a greater forward development of the crest, so that the flattened area of the top of the skull is "pinched in" to a greater degree than in *M. pascuali,* and a median ridge is, in contrast, formed anterior to the area of the parietal foramen, which is reduced almost to the vanishing point. The posterior flanges of the postorbitals which clamp in upon either side of the parietals here reach farther back than is the case in *M. pascuali*, to extend to a point well back of the parietal foramen. As may be seen from Figure 8, the angle of the dentary is less sharp than in *M. pascuali*, the posterior border of the dentary sloping downward and forward at an angle, rather than descending vertically to the apex. As noted, the tooth count of the cheek battery is somewhat higher than in *M. pascuali*. I find no essential difference in the pattern of the "molars" in unworn teeth of the two species.

DISCUSSION

"Gomphodont" cynodonts, with a masticatory series of cheek teeth, were early discovered in the *Cynognathus* Zone of the early Triassic of South Africa. *Diademodon* (of which *Gomphognathus* and several other generic names are synonyms) is the best known, and has been well described by Watson (1911, 1913), Broili and

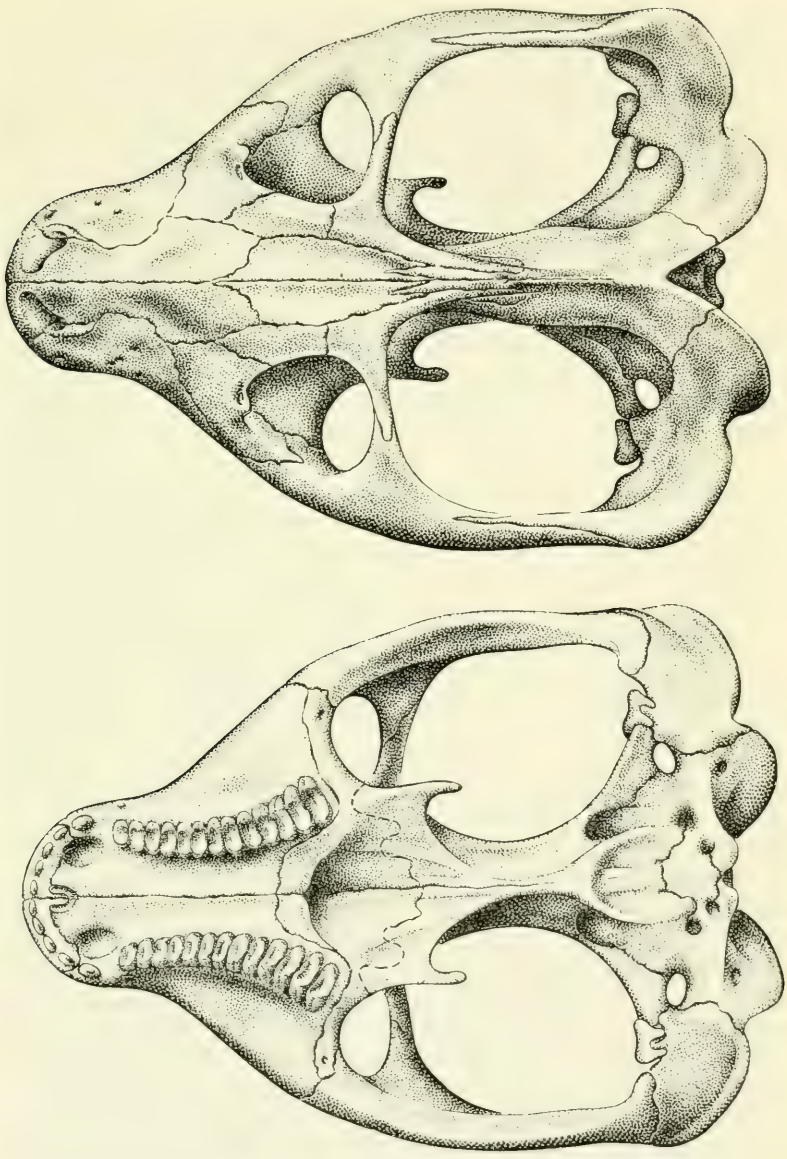

Figure 9. Dorsal and ventral views of the skull of *Massetognathus teruggii*. X ¾.

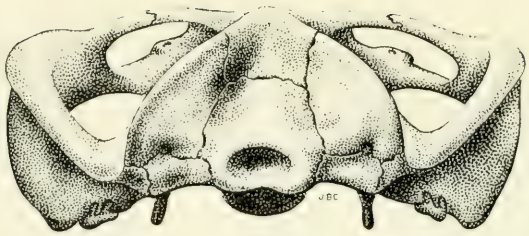

Figure 10. Posterior view of the skull of *Massetognathus teruggii*. X ¾.

Schröder (1935), and most recently by Brink (1955, etc.); *Trirachodon, Protacmon, Trirachodontoides, Gomphodontoides,* and *Inusitatodon* are less well known forms from the *Cynognathus* Zone; a recent discovery is *Cragievarus* (Brink, 1965).

Until recent decades, no remains of gomphodonts were known in other areas or in later Triassic horizons, and it was assumed that the gomphodonts were a short-lived and unimportant branch of the cynodont stock. This, however, was due to our lack of adequate knowledge of Middle Triassic faunas. Explorations from the nineteen-thirties onward, of beds of this age in South America and Africa, are now revealing the fact that the gomphodonts long remained a flourishing group which formed a major component of the Middle Triassic faunas – at least those of the southern continents.

From the Santa María beds of southern Brazil, von Huene (1928, 1942) described *Gomphodontosuchus* and *Traversodon.* From collections made in the Manda beds of East Africa by Parrington and for von Huene have been described *Theropsodon* (Huene, 1950), and *Aleodon, Cricodon,* and *Scalenodon* (Crompton, 1955). In South Africa, the Middle Triassic Molteno beds, long considered barren, have begun to yield fossils to Crompton, including a gomphodont *Scalenodontoides* (Crompton and Ellenberger, 1957). Brink (1963) has recently described a *Diademodon* specimen from Northern Rhodesia at a level which he considers equivalent to the *Cynognathus* Zone, and a new gomphodont, *Luangwa,* from a horizon in the Ntawere Formation which is probably a Molteno equivalent. Large gomphodonts, not yet described, are said to persist into the lower part of the Upper Triassic Redbeds of Basutoland (Crompton, 1964). A recent British expedition resulted in the discovery of further gomphodont material in Northern Rhodesia and Tanganyika. In Argentina a visit by Frenguelli to the Middle Triassic deposits of Ischigualasto produced a

few scraps of gomphodont skull to which Cabrera (1943) gave the name *Exaeretodon* and *Theropsis*. Exploration of this region by a Harvard-Buenos Aires Museum expedition in 1958 revealed the presence of a rich deposit of Middle Triassic vertebrates. As a result of further extensive collections made by the Instituto Lillo of Tucumán, Bonaparte (1962, 1963c) has been able to give a comprehensive description of *Exaeretodon* (with which *Theropsis* proves to be synonymous), and has described two further genera of gomphodonts, *Proexaeretodon* and *Ischignathus* (Bonaparte, 1963d, 1963a). Sr. Bonaparte informs me that he has under description a small diademodont gomphodont from the early Triassic Puesto Viejo Formation of southern Mendoza Province.

According to Dr. Donald Baird, a gomphodont, as yet undescribed, is present in the lower beds of the Newark series of Nova Scotia – the only gomphodont as yet reported from the Northern Hemisphere.

Most recent of gomphodont-bearing faunas to be discovered is that of the Chañares Formation. Forms of this nature are here exceedingly abundant, and, as seen in the field, appear to make up a very large proportion (? one-half) of the total number of specimens recovered. In the small fraction of our collection now available for study there appear to be at least two further distinct genera present, in addition to the forms described above.

The gomphodonts are obviously an herbivorous side branch of the advanced cynodont stock. The circumstances which led to this radical departure from the typically carnivorous mode of life of other cynodonts and, indeed, of all other theriodonts generally, are far from clear. In the late Permian a host of dicynodonts, large and small, were the typical herbivores of the times; as anyone who has collected in the *Endothiodon* or *Cistecephalus* zones of South Africa knows, 90 per cent or so of all specimens found in these beds are members of the dicynodont group. By the time we reach the *Cynognathus* Zone, the dicynodonts are much reduced in numbers and variety, and survive then and later in the Triassic only in the form of such large types as *Kannemeyeria, Ischigualastia,* and *Placerias*. In such typical Middle Triassic faunas as those of Ischigualasto and Santa María, the common herbivores are, instead, of two types in about equal numbers – rhynchosaurs and gomphodonts. In the Chañares fauna we are dealing with an earlier Meso-Triassic stage. Rhynchosaurs must have been in existence (a few ancestral types are found in the *Cynognathus* Zone fauna), but presumably were little developed. (We have found no trace of a rhynchosaur in the sample of the collection currently

available to us, and saw no sure rhynchosaur material while collecting.) Gomphodonts are extremely abundant and apparently varied and, in the way of percentages, occupy much the same position in the Chañares that the dicynodonts did in the Upper Permian. Seemingly, it was only later in the Middle Triassic that rhynchosaurs became fully evolved and came to rival the gomphodonts in numbers.

Judging by the very considerable number of new forms and the amount of new data unearthed during the last few years, we are currently undergoing, so to speak, an explosive period in our acquisition of knowledge concerning gomphodonts. For this reason, and because our knowledge of many of the forms concerned is very incomplete, it is inadvisable at this time to attempt any comprehensive study of gomphodont classification and phylogeny. Pertinent facts, however, may be discussed.

In 1954 Haughton and Brink included all African forms then known in the Diademodontidae. In our 1956 classification of therapsids, Watson and I included all known gomphodonts except *Gomphodontosuchus* in the single family Diademodontidae, and I followed the same pattern in my "Osteology of the Reptiles," published the same year. Lehman, in 1961, in the Piveteau "Traité" also included all gomphodonts (including *Gomphodontosuchus*) in the Diademodontidae, although effecting a subdivision into subfamilies.[1] Von Huene, however, had erected a second family, Traversodontidae, for the Brazilian genera *Traversodon* and *Gomphodontosuchus,* and Crompton and Ellenberger advocated a division of the gomphodonts into two major groups, Diademodontidae and Traversodontidae.

Study of South American gomphodonts brought me in 1961, in contrast to my earlier opinion, to the conclusion that diademodonts and traversodonts (to which *Exaeretodon* obviously belonged) were distinct groups, but also to feel that the *Trirachodon-Cricodon* tooth type indicated the presence of a third group. Bonaparte (1963b) advocated two families, but (*contra* Crompton) would include *Gomphodontosuchus,* as well as the newly discovered Ischigualasto genera, in the Traversodontidae. Brink (1963) would unite these families into a superfamily Gomphodontoidea (*melior* Diademodontoidea?) of advanced cynodonts, in contrast to the carnivores – superfamily Cynognathoidea.

[1] His term "Eudiademodontinae" is, of course, inadmissable, not being based on the name of a genus.

Actually, it would seem, on the basis of present knowledge, that three, rather than two, groups of gomphodonts are present in the Lower and Middle Triassic.

Diademodontidae

Here I would place a series of *Cynognathus* Zone forms typified by *Diademodon,* and a series of named genera identical or closely related, including: *Cyclogomphodon, ?Cynochampsa, Diastemodon, Gomphodontoides, Gomphognathus, Microhelodon, Octagomphus,* and *Protacmon.* The entire anatomy is, as mentioned above, adequately known only in *Diademodon.*

The skull is relatively long, as in typical cynognathids, with a rather long and slender facial region, and with the greatest width toward the posterior end. The squamosal is deeply incised medial to the external auditory meatus, giving a V-shaped dorsal outline to the bone in posterior view; this is quite in contrast to the condition in primitive cynodonts and even cynognathids, in which the two portions of the squamosal are broadly connected at the posterior margin of the temporal fenestra. In cynognathids the skull shape, as seen from above, is that of an isosceles triangle, the breadth gradually increasing backward to its maximum at the posterior end of the zygoma, whereas in diademodonts there is a major increase in width at the orbits, so that the zygomatic arches lie nearly parallel to the main axis of the skull for their entire lengths. The arches are deep, and are mainly formed by the jugals; the squamosals have but a narrow external exposure posteriorly and dorsally. A peculiar feature is a prominent ventral flange below the orbit formed by the jugal. In contrast to some cynognathids there persists in *Diademodon* (but not in *Protacmon*) a primitive condition in that the pterygoid-epipterygoid bar extends back to the quadrate. Certain of the features here listed for *Diademodon* appear to be present in gomphodonts generally; however, the proportions of the "muzzle" are variable, the ventral jugal flange may be absent in some groups, and a broader external exposure of the squamosal is reported in some cases.

Four incisors and a stout canine are present above and below; beginning after a short diastema, the diademodont dentition includes a long row of cheek teeth on either side, the two tooth rows diverging with an outward curvature posteriorly. Thirteen or more cheek teeth may be present; here and in at least certain gomphodonts, teeth may be added posteriorly to the cheek battery during "maturity," and in *Diademodon* small anterior teeth may

be lost and their alveoli closed. The most anterior cheek teeth are peg-like, the most posterior retain a primitive, laterally compressed shape like that of carnivorous cynodonts. The main portion of the dental battery consists of gomphodont "grinders." Here, as in other gomphodonts, there is a strong tendency for the development of rows of small bead-like denticulations along the ridges and cusps of the "molars"; however, these rapidly disappear with wear and are seldom seen, except in teeth in process of eruption. The evolution of the typical "molars" appears to have taken place by an inward growth, from the original compressed carnivore tooth type, of a "heel" overlapping the lower teeth. The original longitudinal tooth line is represented by two stout cusps along the outer margin; variable cusps may be developed medially. There may be some development of small cusps along anterior and posterior margins. A low ridge develops crossing the center of the "heel" from side to side; this, when unworn, shows a row of tiny denticles, but never a developed cusp. The lower "molars" are circular to subquadrate in shape, with a ring of cusps and cuspules surrounding a central basin. There is some suggestion of comparison with the upper "molars" in that the marginal cusps tend to be more highly developed on the medial and lateral margins, and there is some development of a transverse ridge crossing the basin.

The diademodont tooth type is, as far as known, mainly confined to forms from the *Cynognathus* Zone of South Africa. However, Crompton (1955: 656-659, fig. 14 A-D) has described fragmentary jaws from the Manda beds with mandibular "molars" of diademodont pattern. Further, the imperfect skull and jaws from these same beds which form the type of *Aleodon brachyrhamphus* (Crompton, 1955) are suggestive, as Crompton notes, of diademodont relationships, but the teeth are so worn that almost nothing can be made of their pattern.

Trirachodontidae

Trirachodon and *Trirachodontoides* of the *Cynognathus* Zone and *Cricodon* of the Manda beds are forms with a dentition of very distinctive type. There are ten to eleven cheek teeth in *Cricodon*, but only six reported in *Trirachodon*. The cheek tooth rows are nearly straight, but with a slight outward curvature posteriorly in *Cricodon*. In this genus the most anterior cheek teeth are small subcircular "premolars" and, at least in the lower jaw, the most posterior teeth, as in *Diademodon*, "revert" to the narrow cynognathid type. In the *Cynognathus* Zone forms the lower

"molars" are unknown. The upper cheek teeth of *Trirachodon* and both uppers and lowers of *Cricodon* are transversely broadened, but narrow anteroposteriorly. There is a single internal cusp and a single external one, and connecting the two a transverse ridge which with wear develops a prominent longitudinal cusp.

It seems clear that this tooth type has developed independently of that of the diademodonts, by medial lateral development from an ancestral type with but a single major cusp; the diademodont type, on the other hand, expanded laterally from a tooth with greater anteroposterior length. Both Crompton and Ellenberger (1957) and Bonaparte (1963d) would include these forms in the Traversodontidae. But while the upper "molars" of typical traversodonts might perhaps be derivable from the type seen in the present group, I think it is impossible to conceive of the lower "molars" of the traversodonts having been derived from the radically different type seen in *Cricodon* and presumably present in *Trirachodon*.

A minor but perhaps significant feature suggesting at least a distant trirachodont-diademodont relationship is the presence in *Trirachodon* of a suborbital process of the jugal comparable to that of *Diademodon* and *Protacmon*.

Probably of no significance is the fact that the fragment of skull from the Upper Triassic Redbeds named *Tritheledon* by Broom (1912) shows a row of transversely widened multicuspidate teeth, somewhat suggestive of a trirachodont.

Traversodontidae

At present this family (as here restricted) definitely includes two African forms – *Scalenodon* of the Manda beds and *Scalenodontoides* of the Molteno – and a series of South American forms – *Traversodon* from Santa María, *Exaeretodon, Proexaeretodon,* and *Ischignathus* from Ischigualasto, and from the Chañares the two species of *Massetognathus* described above, as well as other forms to be described later. Many of these are incompletely known – *Scalenodontoides* from a lower jaw alone. *Scalenodon* from numerous but fragmentary remains, *Traversodon* from isolated elements from which von Huene has restored a skull; *Proexaeretodon* and *Ischignathus* are represented by incompletely preserved skulls. As yet *Exaeretodon* and *Massetognathus* are the only traversodontids in which adequate skull material is known. Considerable variation in skull structure appears to have been present in the group. All appear to have had, as seemingly in gomphodonts generally, zygomatic arches placed far laterally in a plane parallel to the long

axis of the skull. In general the muzzle is narrow; only in *Massetognathus,* as far as known, do we find a "swollen" maxillary region. In all forms where data are available, the angular process of the dentary is more pronounced than in other cynodonts (including *Diademodon*) and the angular-surangular more exposed laterally. The number of cheek teeth is variable – 8 maxillary teeth, for example, are figured in *Scalenodon* and *Traversodon,* 9 in *Exaeretodon,* 11 in *Proexaeretodon,* 7 in *Ischignathus,* 11 to 15, as noted, in *Massetognathus.*

The "molars," and most especially those of the mandible, with a pair of prominent crests across the anterior border (behind which is a broad "heel"), are the most clearly diagnostic feature of the group. The mandibular teeth are not at all comparable with those of *Cricodon* (or those expected in *Trirachodon*), and offer a major reason for separating those genera from the Traversodontidae.

As far as they are known in members of the South American fauna, the upper "molars" are nearly equally distinctive. There are here two external cusps, the posterior the major one; a prominent transverse ridge along the posterior margin, with a typical development of two cusps toward and at the internal edge; anterior to the posterior crest a concave basin, bounded in front and laterally by a ridge much lower than that behind. The cheek teeth are set closely in series, and even in *Massetognathus* each tooth "shoulders" slightly into the one ahead somewhat medial to the lateral border. This "shouldering" is much more pronounced in *Proexaeretodon* and *Exaeretodon,* so that in the latter genus the tooth appears to consist of two portions, external and internal, set at a considerable angle to one another.

Of the two African forms, *Scalenodon* and *Scalenodontoides,* definitely assignable to the traversodonts, both exhibit lower "molar" patterns characteristic of the family. The upper dentition is unknown in the latter genus, but it is present and well described by Crompton in the former. The maxillary "molars" are basically comparable to those of South American forms, but differ in that there is but a single external cusp, without development of the accessory anterior one, and, further, in that the prominent transverse ridge, bearing two cusps toward and at the inner margin, lies not at the posterior border of the tooth but some distance anterior to it. These differences suggest that *Scalenodon* is rather more primitive than the described South American forms. Possibly we may see here a stage in the evolution of the traversodont upper "molar" from one resembling that of *Trirachodon,* but as remarked

above, such an ancestry seems out of the question as regards the lower cheek teeth.

However, there is evidence in the Manda beds of a form with more advanced upper "molars" – this is represented by a maxilla which Crompton (1955: 659-660, fig. 14 E) compared tentatively with the Brazilian *Gomphodontosuchus,* but which is obviously distinct (there are alveoli for at least ten cheek teeth, whereas the short-jawed *Gomphodontosuchus* has but six). The two "molars" preserved are somewhat worn, but show definitely the presence of two external cusps, a central basin, a low, crenulated, anterior transverse ridge, and a high posterior one. Further, there is a slight posterior marginal concavity on each tooth, indicating a beginning of the "shouldering" which became more prominent in some of the Argentinian genera. It appears probable that we are dealing with a form closely related to, and not impossibly belonging to the genus *Massetognathus.* Significant in this connection is the fact that in this specimen there is, as Crompton notes, a pronounced outward "bulge" of the maxilla lateral to the tooth row, as in *Massetognathus* but not reported in any other described gomphodont.

Forms of doubtful assignment

Apart from genera which seem clearly to belong to one or another of the three groups distinguished above, there are a number of forms which cannot be assigned, mainly because of lack of knowledge of molar pattern.

Inusitatodon (Brink and Kitching, 1953) is a small *Cynognathus* Zone form represented by an incomplete skull. The jaws are tightly locked and the crown pattern of the cheek dental battery – which includes two "premolars" and apparently eight "molars" – is unknown. Brink and Kitching compare the skull with that of *Diademodon* in various regards, but, without giving reasons for this, state that *Trirachodon* is the closest relative.

In the newly described *Cragievarus* (Brink, 1965) from the *Cynognathus* Zone, the cheek tooth pattern is, unfortunately, not described. The "molars" are subquadrate in outline, suggesting reference to the Diademodontidae, and Brink notes various points of agreement with *Diademodon.* However, the cheek tooth row is short (? nine teeth above, seven below), the skull lacks the sharp expansion in width at the orbits usual in gomphodonts, the zygomatic arch is weak, the jugal lacks the ventral process seen in *Diademodon* and *Protacmon,* and the angular process of the dentary is less developed than in typical gomphodonts. Possibly

this form is a primitive but somewhat aberrant diademodontid.

Luangwa (Brink, 1963: 89-93), from the Ntawere Formation of Northern Rhodesia, is obviously, from its expanded cheek teeth, a gomphodont, but the crown pattern is unknown. The shortness of its tooth row (only five "molars" and a miniscule "premolar") is unmatched, except in *Trirachodon* and *Gomphodontosuchus,* but the shape of its subquadrate "molars" is quite different from those of the former (narrow anteroposteriorly) and from the triangular "molars" of the latter genus. The general skull pattern and the "incipient" ventral jugal process suggest the Diademodontidae; possibly we are dealing with a juvenile. Brink states that its closest ally is *Scalenodon,* but gives no reasons.

Aleodon from the Manda (Crompton, 1955) is, again, surely a gomphodont, but, again, we have almost no data on tooth cusps. The skull is little known. The rather "fat" shape of the "molars" suggests the Diademodontidae.

Theropsodon of the Manda beds was described by von Huene (1950) on the basis of a nearly complete but poorly preserved skull. It is definitely a gomphodont, according to von Huene, but the tooth pattern cannot be determined. Possibly it may be identical with either *Cricodon* or *Scalenodon,* from these same beds, or may represent a true diademodont, of which individual teeth are known to be present there.

Gomphodontosuchus from the Brasilian beds is apparently a somewhat aberrant form, with a short face, short tooth row, and massive jaws. The crown pattern of the "molars" is imperfectly preserved. Watson and I, in 1956, assigned this form to a separate family; Crompton and Ellenberger (1957) assigned it to the diademodonts; Bonaparte advocates a position in the Traversodontidae. The last is perhaps the best suggestion, but better material is needed.

Bonaparte (1963b) has suggested that *Belesodon* of the Santa María beds might prove to be a traversodont. However, the Chañares fauna includes a form, as yet undescribed, which is obviously related and probably antecedent to *Belesodon,* in which teeth of cynognathid type are preserved.

Watson, Kühne, Crompton, and Bonaparte have all successively suggested that the tritylodonts were of gomphodont derivation. This may well be the case. In no other therapsid group do we find any appreciable trend for the development of multicuspidate molars. In forms such as *Ischignathus* we find a shortened, compact, "molar" series and a considerable postcanine diastema – features to be sought in a tritylodont ancestor. But although

Crompton has hopefully pointed out that it would be possible to derive tritylodont molars from those of traversodonts, there is still a very considerable structural gap to be bridged. It is to be hoped that further exploration of Middle Triassic deposits will yield forms bridging this gap.

A further possibility is that the gomphodonts may be in some way related to the ancestry of the monotremes. Their ancestry is a complete blank (despite a suggestion at one time of docodont relationships) and it is generally felt that they probably evolved from therapsids of some sort quite separately from other mammals. The curiously multicuspidate "molars" of the forms here described are suggestive in general (although not in detail) of the likewise multicuspidate molars of *Ornithorhynchus*. It may well be that monotremes are descended from gomphodonts of some sort.

LITERATURE CITED

ATTRIDGE, J., H. W. BALL, A. J. CHARIG, and C. B. COX
1964. The British Museum (Natural History) — University of London joint paleontological expedition to Northern Rhodesia and Tanganyika, 1963. Nature, **201**: 445-449.

BONAPARTE, J. F.
1962. Descripción del cráneo y mandíbula de *Exaeretodon frenguellii*, Cabrera y su comparación con Diademodontidae, Tritylodontidae y los cinodontes sudamericanos. Publ. Mus. Munic. Cienc. Nat. Tradic. Mar del Plata, **1**: 135-202.
1963a. Descripción de *Ischignathus sudamericanus* n. gen. n. sp., nuevo cinodonte gonfodonte del Triásico Medio superior de San Juan, Argentina. Acta Geol. Lilloana, **4**: 111-118.
1963b. La familia Traversodontidae. Acta Geol. Lilloana, **4**: 163-194.
1963c. Descripción del esqueleto postcraneano de *Exaeretodon*. Acta Geol. Lilloana, **4**: 5-52.
1963d. Un nuevo cinodonte gonfodonte del Triásico Medio superior de San Juan, *Proexaeretodon vincei* n. gen., n. sp. Acta Geol. Lilloana, **4**: 129-133.

BRINK, A. S.
1955. A study on the skeleton of *Diademodon*. Palaeont. Afr., **3**: 3-39.
1963. Two cynodonts from the Ntawere Formation in the Luangwa Valley of Northern Rhodesia. Palaeont. Afr., **8**: 77-96.
1965. A new gomphodont from the *Cynognathus* zone of South Africa. Palaeont, Afr., **9**: 97-105.

BRINK, A. S. and J. W. KITCHING
1953. On some new *Cynognathus* zone specimens. Palaeont. Afr., **1**: 29-48.

Broili, F. and J. Schroeder

1934. Beobachtungen an Wirbeltieren der Karrooformation. II. Über den Cynodontier *Tribolodon frerensis* Seeley. Sitzungsber. Bayer. Akad. Wiss. München, 1934: 163-190.

1935. Beobachtungen an Wirbeltieren der Karrooformation. IX. Über den Schädel von *Gomphognathus* Seeley. Sitzungsber. Bayer. Akad. Wiss. München, 1935: 115-182.

Broom, R.

1912. On a new type of cynodont from the Stormberg. Ann. S. Afr. Mus., **7**: 334-336, pl. XXII.

Cabrera, A.

1943. El primer hallazgo de terápsidos en la Argentina. Notas Mus. La Plata, Paleont., **8**: 317-331.

Crompton, A. W.

1955. On some Triassic cynodonts from Tanganyika. Proc. Zool. Soc. London, **125**: 617-669.

1964. A preliminary description of a new mammal from the Upper Triassic of South Africa. Proc. Zool. Soc. London, **142**: 441-452.

Crompton, A. W. and F. Ellenberger

1957. On a new cynodont from the Molteno beds and the origin of the tritylodonts. Ann. S. Afr. Mus., **44**: 1-14.

Haughton, S. H. and A. S. Brink

1954. A bibliographical list of Reptilia from the Karroo beds of Africa. Palaeont. Afr., **2**: 1-187.

Huene, F. von

1928. Ein Cynodontier aus der Trias Brasiliens. Centralbl. Min. Geol. Paläont., 1928, Abt. B: 251-270.

1942. Die fossilen Reptilien der südamerikanischen Gondwanalandes. Munich, 332 pp.

1950. Die Theriodontier des ostafrikanischen Ruhuhu-Gebietes in der Tübinger Sammlung. Neues Jahrb. Geol. Palaeont., Abh., **92**: 47-136.

1956. Paläontologie und Phylogenie der niederen Tetrapoden. Jena, 716 pp.

Lehman, J. P.

1961. Cynodontia. *In:* Triaté de Paleontologie, ed. J. Piveteau, VI, vol. I: 140-191.

Romer, A. S.

1956. Osteology of the reptiles. Chicago, 772 pp.

1961. Synapsid evolution and dentition. *In:* International colloquium on the evolution of mammals. Kon. Vlaamse Acad. Wetensch. Lett. Sch. Kunster België, Brussels, 1961, Part 1: 9-56.

1966. The Chañares (Argentina) Triassic reptile fauna. I. Introduction. Breviora, No. 247: 1-14.

ROMER, A. S. and J. A. JENSEN
1966. The Chañares (Argentina) Triassic reptile fauna. II. Sketch of the geology of the Río Chañares-Río Gualo region. Breviora, No. 252: 1-20.
WATSON, D. M. S.
1911. The skull of *Diademodon* with notes on those of some other cynodonts. Ann. Mag. Nat. Hist., (8)**8**: 293-330.
1913. Further notes on the skull, brain, and organs of special sense of *Diademodon*. Ann. Mag. Nat. Hist., (8)**12**: 217-228.
1920. On the Cynodontia. Ann. Mag. Nat. Hist., (9)**6**: 506-524.
WATSON, D. M. S. and A. S. ROMER
1956. A classification of therapsid reptiles. Bull. Mus. Comp. Zool., **114**: 37-89.

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